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# ELEVEN NEW SPECIES OF FREE-LIVING MARINE NEMATODES OF THE GENUS *HALALAIMUS* DE MAN, 1888 (NEMATODA: ENOPLIDA) FROM FLORIDA WITH KEYS TO THE SPECIES

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**ABSTRACT.** The genus *Halalaimus* is reviewed and divided into four groups based on characters of the male. Characters used to separate the groups of males include presence or absence of caudal alae and the presence or absence of a precloacal sensillum and/or pore. Ten new species are described from St. Andrew Bay, Bay County, Florida, and *H. gerlachi* n. sp. is proposed for *H. gracilis* sensu Gerlach, 1967. New species from St. Andrew Bay are *H. thalassinus*, *H. tarjani*, *H. bayensis*, *H. bulbocaudatus*, *H. variabilis*, *H. paracomatus*, *H. americanus*, *H. floridanus*, *H. brimi*, and *H. paraflletcheri*. Keys to the species of each group are provided based on characters of the male. A key to the females of the genus is also provided.

## INTRODUCTION

De Man (1888) erected the genus *Halalaimus* to accommodate a species of free-living marine nematode from the North Sea. The genus *Halalaimus* was differentiated from other genera on the basis of the extremely elongated and longitudinally orientated amphid. The head region of the type species, *Halalaimus gracilis* De Man, 1888, possessed three circles of sensilla. The first circle of sensilla contained six setae (inner labial sensilla), the second circle contained six setae (outer labial sensilla), and the third circle contained four setae (cephalic sensilla). The cuticle was thick and not transversely striated except for the caudal region of the male where there was a series of coarse transverse striations restricted to the lateral fields. A buccal cavity was absent. The esophagus was long and narrow anteriorly and broad posteriorly, and it followed the form of the anterior part of the body which tapers significantly from the esophago-intestinal junction to the attenuated anterior extremity.

Southern (1914) erected the genus *Nuada* for the species *Nuada leptosoma* Southern, 1914 from the coast of Ireland. The genus *Nuada* was characterized by a slender body, thick cuticle, thin-walled head region, four submedian cephalic setae (questioned by Southern, 1914), and the absence of amphids. *N. leptosoma* was represented by two specimens, a male and a female. The four submedian cephalic setae appeared to be present in one specimen and were absent from the other specimen.

Cobb (1920) erected the genus *Tynnodora* for a species of free-living marine nematode, *Tynnodora pachydermata* Cobb, 1920, from Key West, Florida. This species has a circle of outer labial sensilla and a circle of cephalic sensilla (6 + 4) in close proximity to one another, whereas the inner labial sensilla were absent or not observable.

Filipjev (1927) recognized the three genera, *Halalaimus* De Man, 1888; *Nuada* Southern, 1914; and *Tynno-*

*dora* Cobb, 1920; and described new species in each genus. He described *Nuada* as having two circles of sensilla close together in the head region and an amphid similar to that of *Halalaimus*. He stated reasons for considering *Nuada* and *Tynnodora* as subgenera of *Halalaimus* and suggested that *Halalaimus ponticus* Filipjev, 1922 represented a new subgenus of *Halalaimus* or a new genus.

Stekhoven (1935) placed *Nuada* in synonymy with the genus *Halalaimus*, and Allgen (1953) then placed *Nuada* as a subgenus of *Halalaimus*. Wieser (1953) summarized the information regarding the genus *Halalaimus*. He recognized two subgenera, *Halalaimus* s. str. and *Tynnodora* Cobb, 1920, and erected the third subgenus *Pachydora* Wieser, 1953 in which he placed *H. ponticus* and a new species, *Halalaimus clinactericus* Wieser, 1953. He observed that the distinction between the subgenera *Halalaimus* and *Tynnodora* (distance between the anterior and posterior circles of anterior sensilla) is not absolute because transitional species were known. The distinguishing criterion was that the posterior circle of cephalic sensilla in *Tynnodora* was no farther posterior from the circle of outer labial sensilla than the outer labial sensilla were from the anterior end. In the subgenus *Halalaimus* s. str., the circle of cephalic sensilla was farther posterior from the circle of outer labial sensilla than the outer labial sensilla were from the anterior end. Wieser (1953) provided a key to the subgenera and the species within each subgenus. The key emphasized the location and length of the anterior circles of sensilla and the location and length of the amphid.

Mawson (1958) discussed the genus *Halalaimus*, described new species, and constructed a key to the species of the subgenera *Halalaimus* and *Tynnodora*. The keys emphasized the length and position of the anterior sensilla and the shape of the tail. Based on the specimens available to her, Mawson (1958) concluded that the length and position of the amphids was sufficiently variable to render impracticable the use of these characters in a key to the species.

Mawson (1958) also stated that the anterior circles of sensilla were not clear in a number of the specimens available to her, and she assumed that these sensilla were present in the usual numbers.

Timm (1961) described a number of new species of *Halalaimus*. Two of these new species, *Halalaimus setosus* and *Halalaimus filicollis* were described as having six cervical (cephalic) sensilla. Rao (1989) redescribed *H. setosus* and *H. filicollis* and confirmed the presence of six cervical (cephalic) sensilla in these species.

Vitiello (1970) described a number of new species of *Halalaimus* and discussed the characters used in differentiating the species in the genus. His collections yielded a large number of species of *Halalaimus*, but few specimens of each species. Vitiello (1970) expressed the opinion that the difficulty in identifying the species of *Halalaimus* was due to the rather subtle differences between species and the incompleteness of some of the previous descriptions. He observed that the transverse striations in the cuticle are best observed in the caudal region and the area of the posterior end of the amphid. He also observed, as did Mawson (1958), the variability in the position of the amphid in relation to the anterior end of the body and the variability in the length of the amphid. He also stated that the tail is easily broken, and that often it is difficult to determine whether the tail is complete or not. This variability and the subtle differences between species renders specific determination difficult. He also questioned the validity of the subgenus *Pachydora*.

Gerlach and Riemann (1974) placed the subgenus *Tyncnodora* in synonymy with the subgenus *Nuada* and listed the species then known for the three subgenera. Riemann et al. (1970) discussed the morphology of the amphid in the genus *Halalaimus*. Juario (1974) erected a new subgenus, *Nualaimus*, for those species of the genus *Halalaimus* with a distinct circle of inner labial sensilla in addition to the circles of outer labial and cephalic sensilla.

Lorenzen (1981) did not accept the subgenera *Nuada* and *Pachydora*. He also did not recognize the subgenus *Nualaimus*. He placed *Nualaimus* in synonymy with *Halalaimus* because the type species of the genus *Halalaimus* and subgenus *Halalaimus* s. str., *Halalaimus gracilis* De Man, 1888, possessed a circle of inner labial sensilla as well as the outer labial and cephalic sensilla. Juario (1974) had not included *H. gracilis* in the subgenus *Nualaimus*. Therefore, the genus *Halalaimus* is not currently divided into subgenera. *Halalaimus* contains a rather large number of species, and there is a practical reason for subdividing the species into subgenera or groups to make identification easier during ecological studies. However, the traditional subgenera will not be used in this paper in accordance with Lorenzen (1981), nor will new subgenera be erected.

Platt and Warwick (1983) discussed the species of *Halalaimus* from the British Isles and provided figures of

four species. They stated that "the cuticle of some species can be seen to be faintly striated (perhaps all species have striated cuticles but some are beyond the resolving power of the light microscope.)"

The purpose of this paper is to describe the specimens of the genus *Halalaimus* collected from Bay County, Florida and provide a key to the species of the genus *Halalaimus*. In addition, specimens of the genus were obtained from the Smithsonian Institution through the courtesy of Dr. W. Duane Hope and from Dr. Armin C. Tarjan of the University of Florida. Additional specimens were obtained from the U. S. Fish and Wildlife Service Field Office, Panama City, Florida. These specimens were collected as part of a sediment contaminant study of St. Andrew Bay, Florida.

Collections of free-living marine nematodes from estuarine and marine sediments from Bay County, Florida yielded a large number of species of *Halalaimus*, but each species is represented by very few specimens. This is similar to the reports by Mawson (1958) and Vitiello (1970). Many of the specimens examined during this study are not described herein because they were represented by a single specimen or juveniles that could not be associated with a described species.

## MATERIALS AND METHODS

Sediment samples were obtained from shallow water in St. Andrew Bay with corers of various diameters to a depth of 5-10 cm in the sediment. Sediment samples taken by the U. S. Fish and Wildlife Service from deep water in St. Andrew Bay, Bay County, Florida were obtained with a Ponar grab, and a core was taken from the surface of the grab sample. Sediment samples from the Gulf of Mexico were obtained with SCUBA equipment. Nematodes were removed from the sediments by repeated decantation prior to fixation in hot alcohol-formalin-acetic acid, or the entire sediment sample was fixed with 10% formalin in sea water prior to removal of the nematodes. Nematodes were mounted in anhydrous glycerol on Cobb slides. Measurements were made with a calibrated ocular micrometer or were obtained from drawings made with the aid of a drawing tube. Measurements are given in  $\mu\text{m}$  unless otherwise stated, and measurements are given as the mean of the population followed by the range of the population in parentheses. Observations were made with a Nikon Optiphot microscope with Nomarsky Differential Interference Contrast and a Wild M-20 microscope with an oil immersion objective with an N. A. of 1.30.

Only those specimens collected by the author or provided by Dr. Hope, Dr. Tarjan, or the U.S. Fish and Wildlife Service were examined directly. Otherwise, the work is based on descriptions of species provided in the literature.

## RESULTS

The Nomarsky DIC optics made sensilla, lateral cuticular modifications, transverse cuticular striations, and cuticular vermiculations more easily observed. However, the same structures were adequately visible with bright field microscopy, and they probably would not be overlooked.

The body of the members of the genus *Halalaimus* is broadest near the midpoint, and the anterior end tapers greatly from the esophago-intestinal junction to the head. The tail of most species also tapers greatly from the anus to the tail tip. Specimens mounted with supports equal to the width at midbody often yielded specimens in which the head and tail ends were curved upward or downward. This often resulted in the long outer labial and cephalic sensilla following a tortuous course. Accurate measurements of their length was difficult to determine under these circumstances. If the anterior end was turned up or down, the distance of the amphid from the anterior end, the length of the amphid, and the distance between circles of outer labial and cephalic sensilla were difficult to determine accurately.

The anterior end has two or three circles of sensilla that are discernible with a light microscope (Fig. 1). The circle of inner labial sensilla may be present in all species, but may not be discernible with the light microscope when minute. When discernible, the inner labial sensilla vary from papilliform to setiform. When small and papilliform, they may be difficult to observe if the other sensilla obscure them. The circles of outer labial and cephalic sensilla may be close together or far apart, and the length of the sensilla in one circle may be different from that in the other circle. In some instances, it was obvious that the outer labial or cephalic sensilla were broken at the junction with the cuticle.

In general, the cuticle is thin from the anterior end to the level of the cephalic sensilla. The cuticle posterior to the cephalic sensilla is greatly thickened and remains so to the junction of the conical and cylindrical parts of the tail. Setiform cervical, somatic, and caudal sensilla are present in two species, and some species have small, widely spaced pits in the cuticle (Fig. 1). These pits are located sublaterally and begin just posterior to, or at the level of, the posterior end of the amphid and may extend the length of the body. A narrow duct penetrates the cuticle from the base of each pit.

The cuticle of the body may be smooth or have very fine transverse striations. As stated by others, these striations are often best observed at the posterior end of the amphid or in the anal region of the body. In a few species observed during this study, the striations appeared to become minute punctations in the midbody or precloacal region of the male or preanal region in the female.

The cuticle of the conical part of the tail may be smooth or have fine transverse striations in both sexes. Males may have a prominent pattern of broad, elongate elaborations called vermiculations (Fig. 2) which have not been observed in females. These vermiculations appear to be internal and may be restricted to the ventral surface or may occur both ventrally and dorsally to the lateral line. The cylindrical part of the tail may have transverse striations that extend almost to the tail tip (Fig. 2). These striations are more prominent than the transverse striations of the body or conical part of the tail and are referred to as "coarse" striations.

The appearance of the lateral field on each side of the body in some species may be modified to present the appearance of alae (Fig. 2). Gerlach (1967) referred to this modification as "wings." The examination of this modification in whole mounts and coarse transverse sections cut with a razor blade did not reveal a distinct expansion of the cuticle that is characteristic of alae. This cuticular modification appears to be internal, and may not be an ala in the true sense of the term. However, until scanning and transmission electron microscope studies can be performed on this modification, the term ala will be used.

When present on the body, the somatic alae begin between the posterior end of the amphid and the nerve ring over each lateral line and extend the length of the body. When present on the conical part of the tail of females, the alae are extensions of the somatic alae and have no elaborations. The alae on the conical part of the male tail may be present in the absence of somatic alae. If they are present in the male, these lateral alae may have an elaborate scale-like pattern termed "ornamented" (Fig. 2). If the ornamentations are absent, the alae are referred to as "unornamented." When somatic and ornamented caudal alae are present in males, the somatic alae terminate just anterior to the beginning of the caudal alae (Fig. 2).

The tail in the species of *Halalaimus* examined during this study consists of a proximal conical part followed by a cylindrical part that can be filiform or relatively thick. The tail tip is pointed, blunt (expanded or not), or very narrow and divided into two (bifurcate) small terminal appendages (Fig. 3). Caudal glands were observed in the specimens examined. The spinneret was observable in those species with a blunt tail tip but was not observable in those with a bifurcate tail tip.

Males examined during this study may have a single, ventro-median, setiform, precloacal sensillum (Fig. 2); a single, ventro-median, precloacal pore; both the sensillum and the pore; or the sensillum and pore may be absent. When present, the pore has a duct that penetrates the cuticle and turns anteriorly in the body. These structures have been described in other species of the genus, and the presence or absence of these structures is valuable in differentiating species.

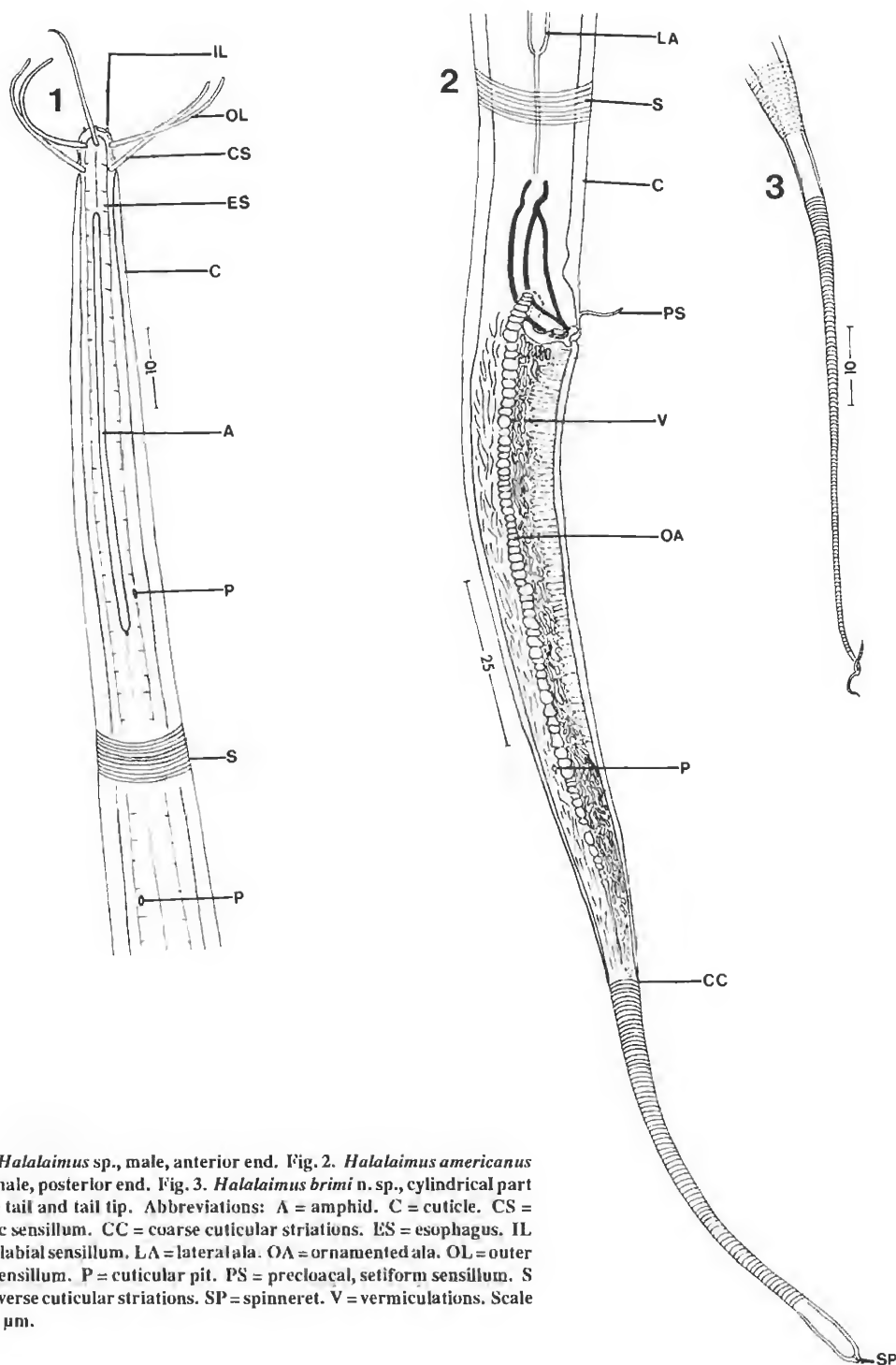


Fig. 1. *Halalaimus* sp., male, anterior end. Fig. 2. *Halalaimus americanus* n. sp., male, posterior end. Fig. 3. *Halalaimus brimi* n. sp., cylindrical part of male tail and tail tip. Abbreviations: A = amphid. C = cuticle. CS = cephalic sensillum. CC = coarse cuticular striations. ES = esophagus. IL = inner labial sensillum. LA = lateral ala. OA = ornamented ala. OL = outer labial sensillum. P = cuticular pit. PS = precloacal, setiform sensillum. S = transverse cuticular striations. SP = spinneret. V = vermiculations. Scale bars in  $\mu\text{m}$ .

Based on the observations made during this study, it appears that the males possess the best characters for differentiating species. The characters of the male emphasized herein are the shape of the tail tip (bifurcate or not), the pattern of cuticular striations on the tail, the presence or absence of somatic transverse cuticular striations, the presence or absence of caudal alae and their ornamentation, the presence or absence of a midventral precloacal sensillum and/or pore, the presence or absence of a pattern of vermiculations in the cuticle in the cloacal region, the shape of the spicules, and the shape and presence or absence of the gubernaculum. The distance of the amphids from the anterior end, the length of the amphid, the length of the outer labial and cephalic sensilla, and the ability to discern the circle of inner labial sensilla with a light microscope are also useful in identifying the species. The method of fixing the specimens did not appear to affect the ability to discern the somatic alae, ornamented or unornamented caudal alae, striations, or vermiculations. These characters were equally visible after formalin or alcohol-formalin-acetic acid fixation.

The characters of the female that appear most reliable are the presence or absence of coarse transverse striations on the cylindrical part of the tail, shape of the tail tip, the presence or absence of somatic transverse cuticular striations, the distance of the amphids from the anterior end, length of the amphids, the ability to discern the circle of inner labial sensilla with a light microscope, and length of the outer labial and cephalic sensilla.

The specimens of the species of *Halalaimus* examined were restricted to those mentioned previously. Comparisons with other species of the genus *Halalaimus* were based on the descriptions in the literature rather than actual examinations of type specimens. This requires that some assumptions be made. It was assumed that inner labial sensilla were not discernible, that transverse cuticular striations were absent, that the somatic and caudal alae were absent, and that a precloacal setiform sensillum and/or pore were absent unless they were mentioned in the description or shown on the figures of the species.

#### Generic Diagnosis - *Halalaimus* De Man, 1888

Enoplida, Oxystominidae, Type species: *Halalaimus gracilis* De Man, 1888. Amphid greatly elongated longitudinally. Anterior and posterior ends of body attenuated. Six inner labial sensilla present or absent (possibly present in all species but not discernible with a light microscope in some). Six outer labial sensilla and four or six (two species) cephalic sensilla present. Cuticle quite thick, abruptly reduced in thickness at level of cephalic sensilla, anus, and again at junction of conical and cylindrical parts of tail; transverse cuticular striations present or absent. Tail conical then cylindrical; tip blunt, or bifurcate. Cylindrical part

of tail with or without transverse cuticular striations. Caudal glands present; spinneret present or undetermined. Species mostly marine and estuarine. Coomans and Jacobs (1983) discuss those species not found in estuarine and marine environments.

The specimens described and discussed herein are divided into groups based on male characters in order to provide some degree of organization and points of reference. A key to the males of the species in each group is given at the end of the account of the species in that group. A separate key to the females of all species is given at the end of the taxonomic section, because they are not as easily separated into groups as the males. Those species of the genus listed as *inquirenda* in Gerlach and Riemann, (1974) are not included in the following keys. A list of the species included in the following discussions and keys to the species of *Halalaimus* follows.

#### Known Species

- Halalaimus alatus* Timm, 1952
- Halalaimus algeriensis* Coomans and Jacobs, 1983
- Halalaimus amphidellus* Vitiello, 1970
- Halalaimus amphistrius* Vitiello, 1970
- Halalaimus anne* Sergeeva, 1972
- Halalaimus brachyaulax* Mawson, 1958
- Halalaimus brevispiculum* Sergeeva, 1973
- Halalaimus capitulatus* Boucher, 1977
- Halalaimus caroliniensis* Chitwood, 1936
- Halalaimus cilicaudatus* Allgen, 1932
- Halalaimus cirrhatus* Gerlach, 1953
- Halalaimus climactericus* Wieser, 1953
- Halalaimus comatus* Wieser, 1953
- Halalaimus cubanus* Andrassy, 1973
- Halalaimus curvicaudatus* Juario, 1974
- Halalaimus delamarei* Vitiello, 1970
- Halalaimus diacros* Mawson, 1958
- Halalaimus diplocephalus* Filipjev, 1927
- Halalaimus filicollis* Timm, 1961
- Halalaimus filicorpus* Vitiello, 1970
- Halalaimus filum* Gerlach, 1962
- Halalaimus fletcheri* Mawson, 1958
- Halalaimus florensens* Gerlach, 1967
- Halalaimus gracilis* De Man, 1888
- Halalaimus horridus* Gerlach, 1956
- Halalaimus isaitshikovi* Filipjev, 1927
- Halalaimus jaltensis* Sergeeva, 1973
- Halalaimus leptoderma* Platonova, 1971
- Halalaimus leptosoma* Southern, 1914
- Halalaimus lineatoides* Timm, 1961
- Halalaimus lineatus* Timm, 1961
- Halalaimus longicaudatus* Filipjev, 1927
- Halalaimus longicollis* Allgen, 1932
- Halalaimus longisetosus* Hopper, 1963

*Halalaimus longistriatus* Timm, 1961  
*Halalaimus lularus* Vitiello, 1970  
*Halalaimus luiculus* Timm, 1961  
*Halalaimus macquariensis* Mawson, 1958  
*Halalaimus marri* Mawson, 1958  
*Halalaimus meyersi* Wieser and Hopper, 1967  
*Halalaimus minisculus* Tchesunov, 1978  
*Halalaimus monstrocaudatus* Vitiello, 1970  
*Halalaimus nigrilapidarius* Boucher, 1977  
*Halalaimus pachyderma* Filipjev, 1927  
*Halalaimus pachydermatus* Cobb, 1920  
*Halalaimus pachydoroides* Vitiello, 1970  
*Halalaimus papillifer* Gerlach, 1956  
*Halalaimus parvus* Chitwood, 1936  
*Halalaimus ponticus* Filipjev, 1922  
*Halalaimus rectispiculatus* Platonova, 1971  
*Halalaimus relatus* Gerlach, 1967  
*Halalaimus sarsi* Gerlach, 1967  
*Halalaimus scleratus* Timm, 1962  
*Halalaimus setosus* Timm, 1961  
*Halalaimus similis* Allgen, 1930  
*Halalaimus sobakini* Sergeeva, 1973

*Halalaimus stammeri* Schneider, 1940  
*Halalaimus striatus* Gerlach, 1956  
*Halalaimus supercirrhatus* Gerlach, 1955  
*Halalaimus tenuicapitatus* Filipjev, 1946  
*Halalaimus terrestris* Gerlach, 1959  
*Halalaimus turbidus* Vitiello, 1970  
*Halalaimus wodjanizkii* Sergeeva, 1972  
*Halalaimus zenkevitchi* Filipjev, 1927

#### New Species Described Herein.

*Halalaimus thalassinus* n. sp.  
*Halalaimus tarjani* n. sp.  
*Halalaimus bayensis* n. sp.  
*Halalaimus bulbocaudatus* n. sp.  
*Halalaimus variabilis* n. sp.  
*Halalaimus paracomatus* n. sp.  
*Halalaimus americanus* n. sp.  
*Halalaimus floridanus* n. sp.  
*Halalaimus gerlachi* n. sp.  
*Halalaimus brimi* n. sp.  
*Halalaimus parafletcheri* n. sp.

#### Artificial Key to the Groups of Males of the Genus *Halalaimus* De Man, 1888.

The male characters used to define the groups are the presence or absence of caudal alae and the presence or absence of a precloacal sensillum and/or precloacal pore. These characters are used in combination to distinguish four artificial groups in the following key:

- |       |  |         |
|-------|--|---------|
| 1.    | Caudal alae present .....                      | 2       |
|       | Caudal alae absent .....                       | 3       |
| 2(1). | Precloacal sensillum and/or pore present ..... | Group 1 |
|       | Precloacal sensillum and/or pore absent .....  | Group 2 |
| 3(1). | Precloacal sensillum and/or pore present ..... | Group 3 |
|       | Precloacal sensillum and/or pore absent .....  | Group 4 |

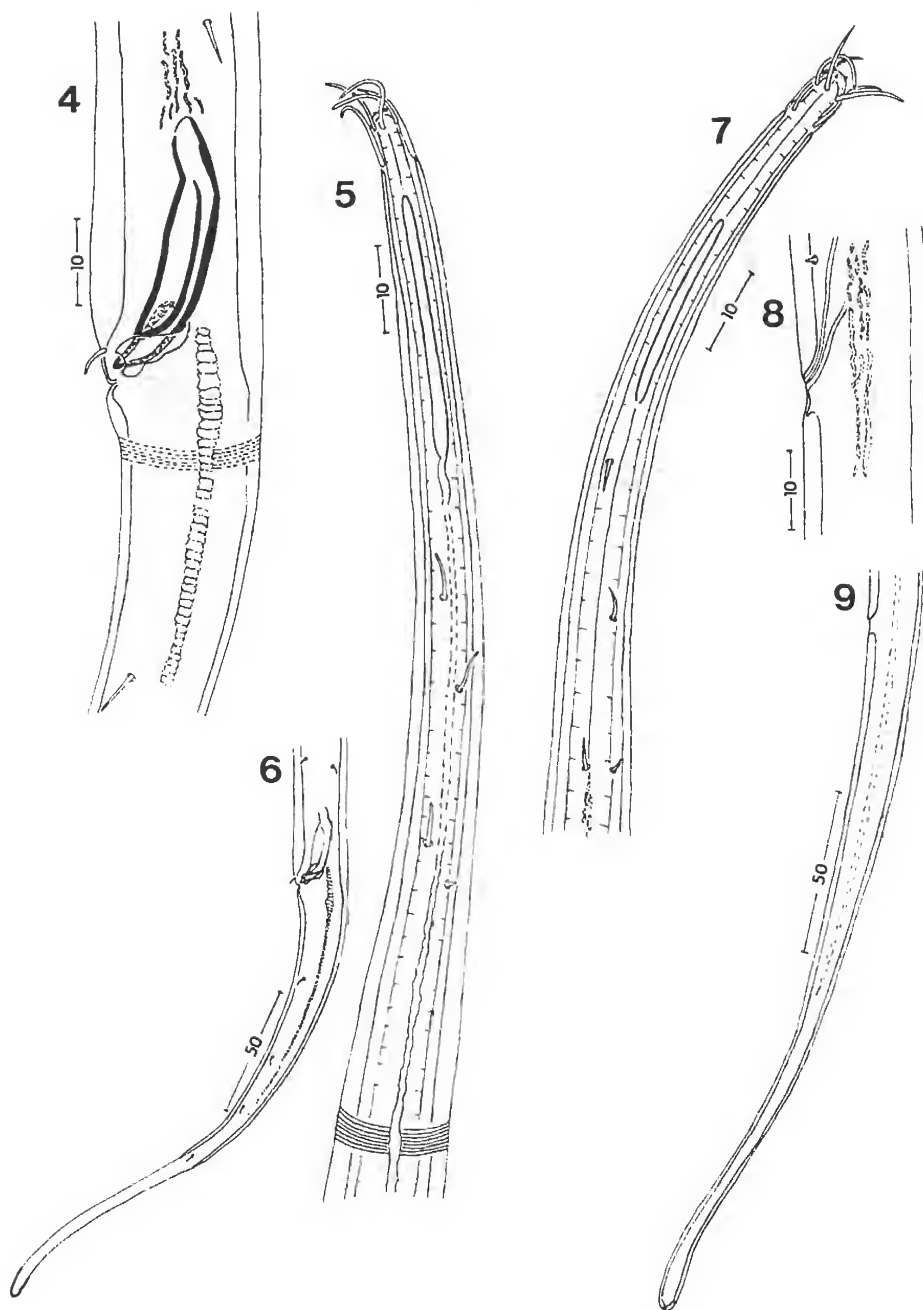
#### Group 1

Males of the species in this group have caudal alae, and a setiform precloacal sensillum and/or pore is present. The known species and those described as new herein have ornamented caudal alae. However, two male specimens of apparently different species were examined that had unornamented caudal alae, but they are not described here because each is represented by a single specimen. Distinctly visible circle of inner labial sensilla present or not discernible. Outer labial sensilla may be longer or shorter than cephalic sensilla, and the two circles are of varying distances apart. Species in this group all have a tail with blunt tip and visible spinneret.

Wieser (1953) described *Halalaimus comatus* on the basis of female specimens collected from the coast of Chile. Mawson (1958) described the male of *H. comatus* from the Antarctic. The male has ornamented caudal alae and a single, ventro-median, precloacal sensillum. *H. comatus* was unique in the presence of these characters. However, the collections from Florida waters yielded a number of additional species with these characters.

#### *Halalaimus thalassinus* n. sp. Figs. 4-9

Cuticle with fine transverse striations. Lateral somatic alae present, begin just posterior to amphid, indistinct at



Figs. 4-9. *Halalaimus thalassinus* n. sp. Fig. 4. Male, cloacal region, left lateral view. Fig. 5. Male, anterior end, left lateral view. Fig. 6. Male, posterior end, left lateral view. Fig. 7. Female, anterior end, left lateral view. Fig. 8. Female, anal region, left lateral view. Fig. 9. Female, posterior end, left lateral view. Scale bars in  $\mu\text{m}$ .

first then more evident, vermiculated anteriorly, smooth over most of body, then vermiculated precloacally in male. Somatic alae terminate just anterior to the cloaca in male, ornamented caudal alae present. Somatic alae terminate postanally in female at junction of conical and cylindrical parts of tail, not vermiculated preanally, and caudal alae not ornamented. Setiform cervical sensilla present from just posterior to amphid to level of strongly defined lateral alae in males, become papilliform on remainder of body, then setiform precloacally and caudally. Setiform cervical sensilla present, somatic and caudal sensilla absent in females. Excretory pore not observed. Inner labial sensilla papilliform. Outer labial and cephalic sensilla equal in length, in two well-separated circles. Males with precloacal setiform sensillum present; pore absent. Cylindrical part of tail with fine transverse striations. Tail tip expanded, blunt; spinneret present.

**Male (n = 1):** Length 2.24 mm. Width at midbody 22. Head diameter 4.2 at level of cephalic sensilla. Outer labial and cephalic sensilla 11 long. Labial surface to amphid 22 and nerve ring 229. Amphid 23 long. Cervical and caudal sensilla 5 long. Esophagus 466 long. Tail 216 long. Width at cloaca 20. Spicules 30 long, alate. Gubernaculum 9.6 long; consists of a plate with keel-like extension between spicules and a cup-shaped part lateral to tip of each spicule.  $a = 101.8$ .  $b = 4.81$ .  $c = 10.4$ .

**Female (n = 1):** Length 2.21 mm. Width at midbody 27. Head diameter 4.8 at level of cephalic sensilla. Outer labial and cephalic sensilla 10 long. Labial surface to amphid 24 and nerve ring 240. Amphid 27 long. Cervical sensilla 5 long. Esophagus 473 long. Tail 213 long. Width at anus 16. Reproductive system amphidelphic; reflexed. Vulva 1.18 mm from anterior end.  $a = 81.9$ .  $b = 4.67$ .  $c = 10.4$ .  $V = 53\%$ .

**Specimens:** Male holotype, USNM 77260; female allotype, USNM 77261.

**Locality:** St. Andrew Bay, Bay County, Florida (85° 42'43"W, 30° 08'33"N) at the National Marine Fisheries Service Laboratory, from a seagrass bed (*Thalassia testudinum*) about 1 meter deep.

**Etymology:** from the Greek *Thalass*, the sea.

**Remarks:** *Halalaimus thalassinus* n. sp. is unique among the species in Group 1 in the possession of cervical, somatic and caudal sensilla in the male and cervical sensilla in the female. The only other species in the genus *Halalaimus* with distinct cervical and caudal sensilla is *Halalaimus delamarei* Vitello, 1970, which has been placed in Group 3. *H. delamarei* does not have caudal alae in the male, the cervical and caudal sensilla are very short, and inner labial sensilla are not discernible.

#### *Halalaimus tarjani* n. sp.

Figs. 10-19

Cuticle with fine transverse striations. Lateral somatic alae not observed. Ornamented caudal alae present in male, absent in female. Inner labial sensilla setiform. Outer labial and cephalic sensilla setiform and unequal in length; cephalic sensilla longer; circles well-separated. Excretory pore not observed. Lateral alae not observed. Males with precloacal sensillum, pore absent; ornamented caudal alae present. Tail conical then cylindrical. Cylindrical part of tail with coarse transverse striations. Tail tip clavate; spinneret present.

**Males (n = 4):** Length 1.09 mm (1.05-1.13). Width at midbody 22.7 (22-24). Head diameter 5.1 (4.4-5.3) at level of cephalic sensilla. Outer labial and/or cephalic sensilla were broken or missing on three males. One male with all sensilla present with outer labials 2.4 long, cephalic sensilla 4.0 long. Cephalic sensilla in holotype 4.8 long. Labial surface to amphid 8.6 (7.8-9.6) and nerve ring 186 (182-190). Amphid 38.8 (38-40) long. Esophagus 371.8 (353-378) long. Tail 159 (154-165) long. Width at cloaca 19 (19-19). Spicules 39 (38-40) long, alate. Gubernaculum 10.0 (9.6-11.0) long, consists of a plate with keel-like extension between spicules and cup-shaped extension lateral to each spicule tip. Vermiculations not observed on conical part of tail.  $a = 46.5$  (46.7-48.2).  $b = 2.93$  (2.88-3.00).  $c = 6.90$  (6.75-7.06).

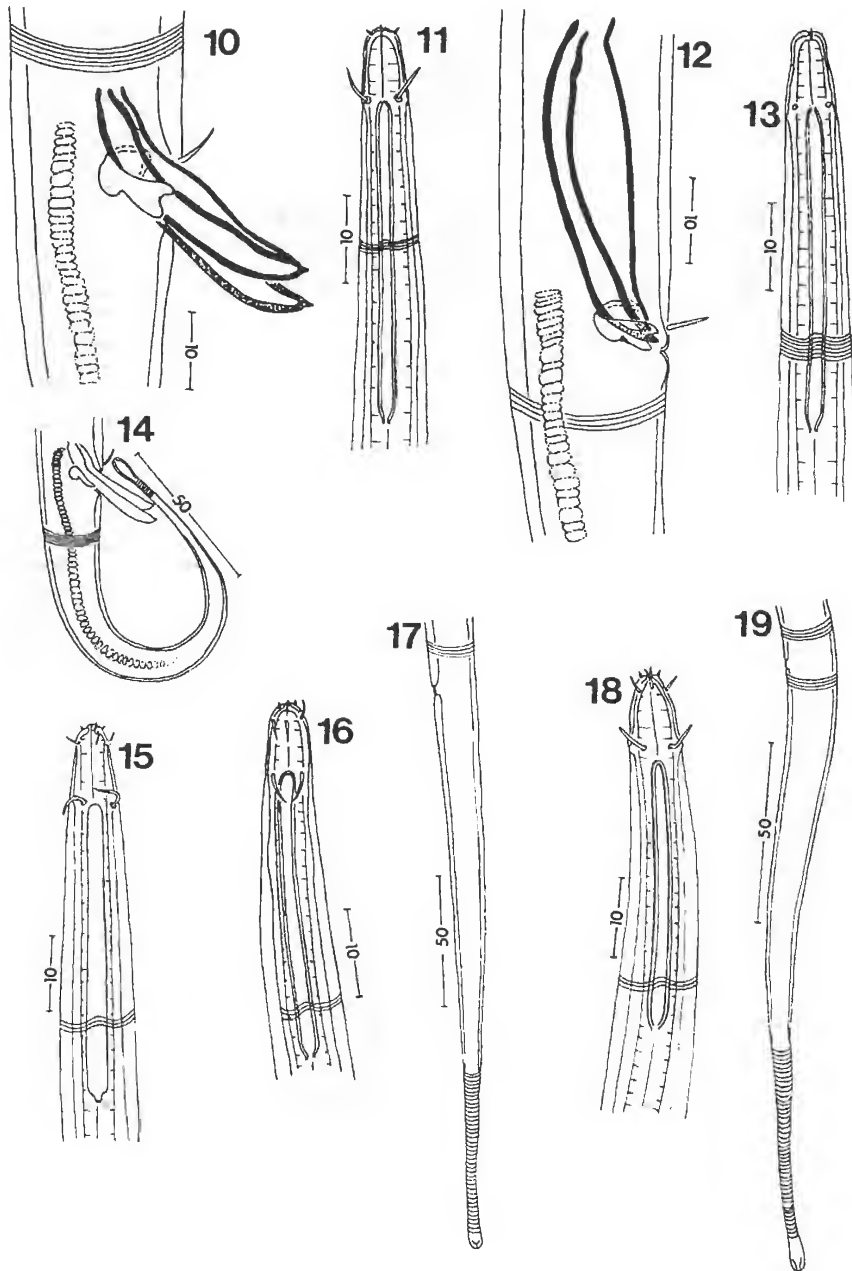
**Females (n = 2):** Length 1.06 mm (1.02-1.09). Width at midbody 33 (29-37). Head diameter 6.4 (6.4-6.4) at level of cephalic sensilla. Outer labial sensilla 2.1 (2.1-2.1) long. Cephalic sensilla 4.3 (4.3-4.3) long. Labial surface to amphid 10 (10-10) and nerve ring 179 (178-180). Amphid 32 (32-32) long. Esophagus 346.5 (321-372) long. Tail 176.5 (171-182) long. Width at anus 15 (14-16). Reproductive system amphidelphic; reflexed. Vulva 589 (567-611) from anterior end.  $a = 32.4$  (29.5-35.2).  $b = 3.06$  (2.93-3.18).  $c = 5.98$  (5.96-6.00).  $V = 56\%$  (56-56).

**Specimens:** Holotype male, USNM 77262; three paratype males, USNM 77263-77265; allotype female, USNM 77497; paratype female USNM 77499.

**Locality:** St. Andrew Bay, Bay County, Florida (85° 39'46"W, 30° 08'34"N) water 13 meters deep, (85° 38'52"W, 30° 07'38"N) water 7.5 meters deep, and (85° 39'46"W, 30° 08'40"N) water 12.2 meters deep.

**Etymology:** Named for Dr. Armen C. Tarjan, University of Florida.

**Remarks:** *Halalaimus tarjani* n. sp. belongs with those species in Group 1 that have discernible inner labial sensilla, ornamented caudal alae, and the cylindrical part of tail has coarse striations. *H. tarjani* n. sp. differs from the only other species with these characters, *Halalaimus bayensis* n. sp. (to be described next), in that the outer labial and cephalic sensilla are much shorter and unequal in length (0.29-0.33 & 0.78-0.92 versus 2.8-3.0 head diameters), the amphid begins much closer to the anterior end (1.7 versus 5.3-6.0 head diameters), the spicules are longer (2.0-2.1



Figs. 10-19. *Halalaimus tarjani* n. sp. Fig. 10. Male, cloacal region, right lateral view. Fig. 11. Male, anterior end, right lateral view. Fig. 12. Male, cloacal region, right lateral view. Fig. 13. Male, anterior end, right lateral view. Fig. 14. Male, posterior end, right lateral view. Fig. 15. Male, anterior end, left lateral view. Fig. 16. Female, anterior end, left lateral view. Fig. 17. Female, posterior end, left lateral view. Fig. 18. Female, anterior end, left lateral view. Fig. 19. Female, posterior end, left lateral view. Scale bars in µm.

versus 1.7 cloacal diameters), and the gubernaculum is of a different shape.

*H. tarjani* n. sp. is also similar to those species of the genus *Halalaimus* with a broad amphid. Wieser (1953) placed those species with a broad amphid (40% of corresponding body diameter at midlength of the amphid) in the subgenus *Pachydora*. This subgenus contained two species, *Halalaimus (Pachydora) ponticus* Filipjev, 1922 and *Halalaimus (Pachydora) climactericus* Wieser, 1953. Vitello (1970) described *Halalaimus pachydoroides* and discussed the relationship between amphid width and corresponding body diameter and demonstrated that the relationship decreases from the anterior to posterior end of the amphid in *H. pachydoroides* and *H. ponticus*.

*H. tarjani* n. sp. also demonstrates this relationship. The amphid is 29.8% (27-32) of the corresponding body diameter anteriorly and 24% (20-27) posteriorly. *H. tarjani* n. sp. females differ from *H. climactericus* females (male unknown) in the presence of coarse transverse striations on the cylindrical part of the tail, presence of discernible inner labial sensilla, and in the longer outer labial and cephalic sensilla (2.1 & 4.3 versus 1.0 and 2.0). *H. tarjani* n. sp. differs from *H. pachydoroides* (Group 4) in the presence of discernible inner labial sensilla, shape of the tail (cylindrical part short, blunt versus cylindrical part long, flagellate), in the greater distance between circles of outer labial and cephalic sensilla (1.1-1.2 versus 0.4 head diameters), and in the shorter length of the tail (males "c" = 6.75-7.06, females "c" = 5.96-6.00 versus males "c" = 4.7-5.0, females "c" = 4.9-6.1). *H. tarjani* n. sp. differs from *H. ponticus* in the presence of a discernible circle of inner labial sensilla, and in the presence of ornamented caudal alae in the male.

***Halalaimus bayensis* n. sp.**

**Figs. 20-27**

Cuticle with fine transverse striations, appear punctate at midbody. Cuticular pits present. Lateral alae not observed. Ornamented caudal alae restricted to conical part of male tail; absent in female. Cuticle in male cloacal region faintly vermiculated on ventral surface in holotype, more distinct in paratype. Inner labial sensilla papilliform. Outer labial and cephalic sensilla equal in length within and between circles; in two well-separated circles. Excretory pore not observed. Males with setiform precloacal sensillum; pore absent. Cylindrical part of tail with coarse transverse striations. Tail tip blunt; spinneret present.

**Males (n = 2):** Length 1.24 mm (1.19-1.28). Width at midbody 20 (19-21). Head diameter 3.6 (3.6-3.6) at level of cephalic sensilla. Outer labial and cephalic sensilla 11.5 (11-12) long. Labial surface to amphid 23.5 (23-24) and nerve ring 184 (182-186). Amphid 48 (46-50) long. Esophagus 302 (296-308) long. Tail 190.5 (189-192) long. Width at

cloaca 14 (14-14). Spicules 24 (24-24) long, alate. Gubernaculum 8 (8-8) long, consists of plate with keel-like extension between spicules and cup-shaped extension lateral to each spicule tip. a = 62.1 (56.7-67.4), b = 4.09 (4.02-4.16), c = 6.49 (6.30-6.67).

**Juvenile female (n = 1):** Length 1.10 mm. Width at midbody 16. Head diameter 3.6 at level of cephalic sensilla. Outer labial and cephalic sensilla 11 long. Labial surface to amphid 37 and nerve ring 158. Amphid 37 long. Esophagus 265 long. Tail 160 long. Width at anus 11. Reproductive system amphidelphic; reflexed. Anterior end to vulva 536. a = 68.8. b = 4.15. c = 6.88. V = 49%.

**Specimens:** Holotype male, USNM 77498; allotype female, USNM 77500.

**Locality:** St. Andrew Bay, Bay County, Florida (85° 39'46"W, 30° 08'40"N and 85° 36'43"W, 30° 06'52"N). Water 9.5 and 12.2 meters deep.

**Etymology:** Named for the geographic locality, Bay County, Florida.

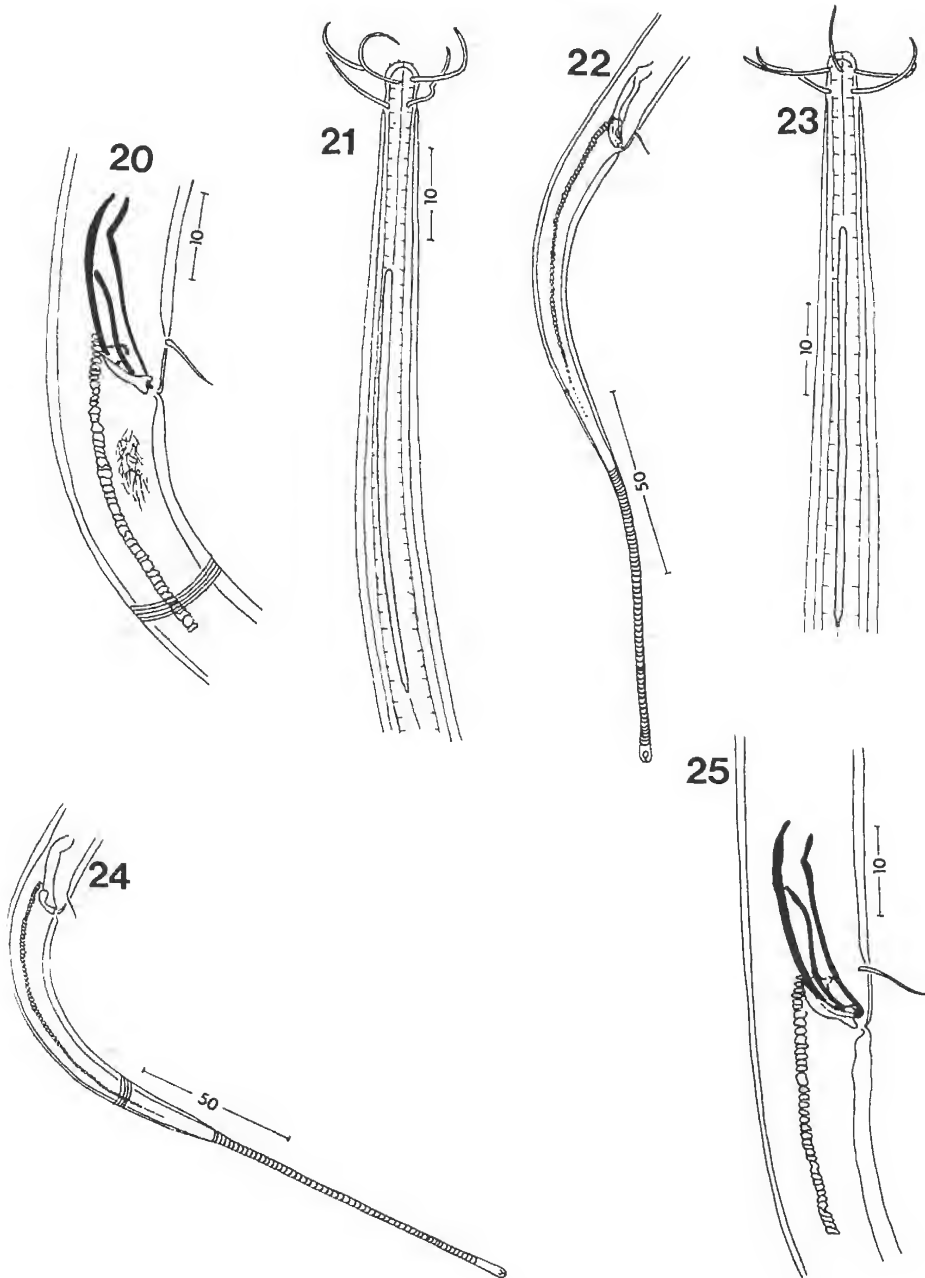
**Remarks:** *Halalaimus bayensis* n. sp. belongs with those species in Group 1 that have a discernible circle of inner labial sensilla, ornamented caudal alae, and the cylindrical part of the tail has coarse transverse striations. *H. bayensis* n. sp. differs from *H. tarjani* n. sp. as described under the remarks section for *H. tarjani* n. sp. *H. bayensis* n. sp. males are also similar to males of *H. variabilis* n. sp. and *H. floridanus* n. sp. (both described below). *H. bayensis* n. sp. differs from *H. variabilis* n. sp. in the presence of a precloacal setiform sensillum, the absence of a precloacal pore, and the presence of discernible inner labial sensilla. *H. bayensis* n. sp. differs from *H. floridanus* n. sp. in the shorter outer labial and cephalic sensilla (2.8-3.0 versus 4.4-4.5 head diameters long), distance from the labial surface to the amphid (5.3-6.0 versus 2.9-3.1 head diameters), length of the tail (13.5-13.7 versus 7.5-9.4 cloacal diameters long), "a" value (56.0-67.4 versus 78.0-89.5), and the presence of discernible inner labial sensilla.

***Halalaimus bulbocaudatus* n. sp.**

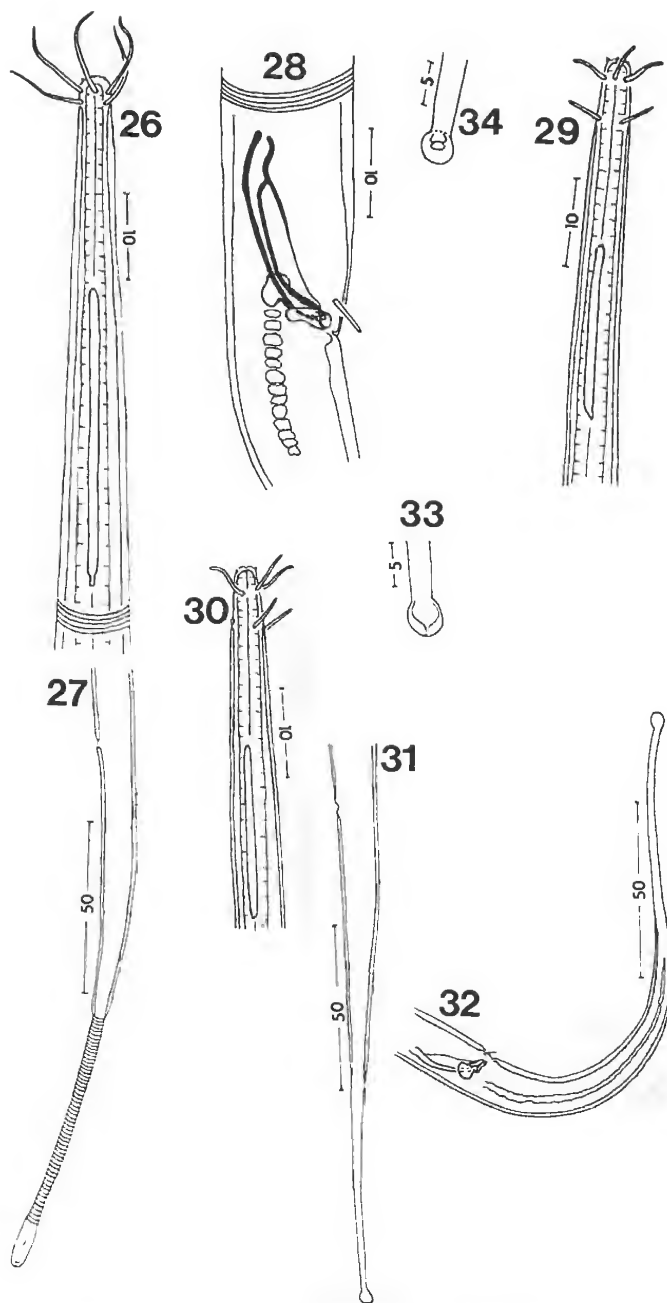
**Figs. 28-34**

Cuticle with faint transverse striations, best observed in precloacal region in male. Lateral somatic alae not observed. Ornamented caudal alae present in male, absent in female. Inner labial sensilla papilliform. Outer labial and cephalic sensilla equal in length, circles well-separated. Amphid relatively short, situated well posterior to cephalic sensilla. Excretory pore not observed. Male with precloacal sensillum; pore absent. Cylindrical part of tail without coarse transverse striations. Tail tip in both sexes with nearly spherical swelling at tip; spinneret present.

**Male (n = 1):** Length 1.16 mm. Width at midbody 20. Head diameter 3.8 at level of cephalic sensilla. Outer labial and cephalic sensilla 4.2 long. Labial surface to amphid 21



Figs. 20-25. *Halalaimus bayensis* n. sp. Fig. 20. Male, cloacal region, right lateral view. Fig. 21. Male, anterior end, right lateral view. Fig. 22. Male, posterior end, right lateral view. Fig. 23. Male, anterior end, right lateral view. Fig. 24. Male, posterior end, right lateral view. Fig. 25. Male, cloacal region, right lateral view. Scale bars in μm.



Figs. 26-27. *Halalaimus bayensis* n. sp. Fig. 26. Juvenile female, anterior end, left lateral view. Fig. 27. Juvenile female, posterior end, left lateral view. Figs. 28-34. *Halalaimus bulbocaudatus* n. sp. Fig. 28. Male, cloacal region, right lateral view. Fig. 29. Male, anterior end, left lateral view. Fig. 30. Female, anterior end, left lateral view. Fig. 31. Female, posterior end, left lateral view. Fig. 32. Male, posterior end, right lateral view. Fig. 33. Female, tail tip. Fig. 34. Male, tail tip. Scale bars in  $\mu\text{m}$ .

and nerve ring 200. Amphid 19 long. Esophagus 334 long. Tail 155 long. Width at cloaca 14. Spicules 23 long. Gubernaculum 8 long, consists of a plate with keel-like extension between spicules and extension lateral to each spicule tip. Postcloacal cuticular vermiculations absent.  $a = 58.0$ .  $b = 3.47$ .  $c = 7.84$ .

**Female** ( $n = 1$ ): Length 1.05 mm. Width at midbody 20. Head diameter 3.8 at level of cephalic sensilla. Outer labial and cephalic sensilla 4.2 long. Labial surface to amphid 20 and nerve ring 184. Amphid 19 long. Esophagus 315 long. Tail 152 long. Width at anus 13. Reproductive system amphidelphic; reflexed. Anterior end to vulva 580.  $a = 50.0$ .  $b = 3.33$ .  $c = 6.91$ .  $V = 55\%$ .

**Specimens:** Holotype male, USNM 77266; allotype female, USNM 77267.

**Locality:** St. Andrew Bay, Bay County, Florida (85° 38' 19"W, 30° 07' 44"N). Water 12.2 meters deep.

**Etymology:** from Latin *bulbo* meaning "a bulb" and Latin *caudatus* meaning "having a tail."

**Remarks:** *Halalaimus bulbocaudatus* n. sp. belongs with those species in Group 1 that have ornamented caudal alae, coarse transverse striations are absent from the cylindrical part of the tail, and the inner labial sensilla are discernible. *H. bulbocaudatus* n. sp. differs from *H. thalassinus* n. sp. in the absence of setiform cervical and caudal sensilla, the presence of a spherical swelling at the tail tip, and the outer labial and cephalic sensilla are shorter (1.1 versus 2.2 head diameters).

A spherical swelling at the tail tip is also present in *Halalaimus similis* Allgen, 1930 (only the female is known), and the same was also described for this species by Bresslau and Stekhoven (1940). Wieser (1953) described *Halalaimus comatus* with a knob-like swelling at the tail tip. Mawson (1958) described the tail tip in specimens of *H. comatus* as swollen in the female and as a distinct spherical swelling in the male similar to that described for *H. similis*.

*H. bulbocaudatus* n. sp. is similar to *H. comatus* in the presence of ornamented caudal alae and a precloacal setiform sensillum in the male and in the absence of coarse transverse striations on the cylindrical part of the tail in both sexes. *H. bulbocaudatus* n. sp. differs from *H. comatus* in the presence of a discernible circle of inner labial sensilla and the greater distance between the circles of outer labial and cephalic sensilla (1.0 head diameter versus 0.23 head diameter). *H. bulbocaudatus* n. sp. females differ from *H. similis* females (males unknown) in the presence of a discernible circle of inner labial sensilla.

#### *Halalaimus variabilis* n. sp.

Figs. 35-43

Cuticle with fine transverse striations, appear punctate in midbody region, gradually become vermiculations anterior to cloaca in male; not present in female. Lateral alae

not observed. Ornamented caudal alae present in male, absent in female. Cuticular pits present for length of body. Inner labial sensilla not discernible. Outer labial and cephalic sensilla equal in length, in two well-separated circles. Excretory pore not observed. Conical part of tail with vermiculations on ventral surface in male, absent in female. Precloacal sensillum absent, precloacal pore present. Cylindrical part of tail with coarse transverse striations in both sexes. Tail tip narrow, blunt; spinneret present.

**Males** ( $n = 2$ ): Length 1.85 mm (1.72-1.97). Width at midbody 22.5 (21-24). Head diameter 5.1 (4.8-5.4) at level of cephalic sensilla. Outer labial and cephalic sensilla 17 (15-19) long. Labial surface to amphid 18.5 (16-21) and nerve ring 208 (200-216). Amphid 53 (38-68) long. Esophagus 381.5 (353-410) long. Tail 203 (198-208) long. Width at cloaca 16.5 (16-17). Spicules 20.5 (19-22) long. Gubernaculum 9.8 (9.6-10.0) long, consists of a plate with a keel-like extension between spicules, and an extension lateral to each spicule tip; distal end cup-shaped.  $a = 82.0$  (81.9-82.1).  $b = 4.84$  (4.80-4.87).  $c = 9.11$  (8.27-9.95).

**Females** ( $n = 2$ ): Length 1.81 mm (1.58-2.03). Width at midbody 26.5 (26-27). Head diameter 5.1 (4.8-5.4) at level of cephalic sensilla. Outer labial and cephalic sensilla 17.5 (17-18) long. Labial surface to amphid 18.5 (16-21) and nerve ring 201 (194-208). Amphid 53 (46-60) long. Esophagus 365.5 (321-410) long. Tail 217.5 (213-222) long. Width at anus 15 (15-15). Reproductive system amphidelphic, reflexed. Vulva 919.5 (844-995) from anterior end.  $a = 68.3$  (58.5-78.1).  $b = 4.94$  (4.92-4.95).  $c = 10.5$  (9.5-11.4).  $V = 51\%$  (49-53).

**Specimens:** Male holotype, USNM 77503; male paratype, USNM 77504; female allotype, USNM 77544.

**Locality:** Mouth of Freshwater Bayou off St. Andrew Bay, Bay County, Florida (85° 39' 00"W, 30° 07' 30"N). Water 2.1 meters deep.

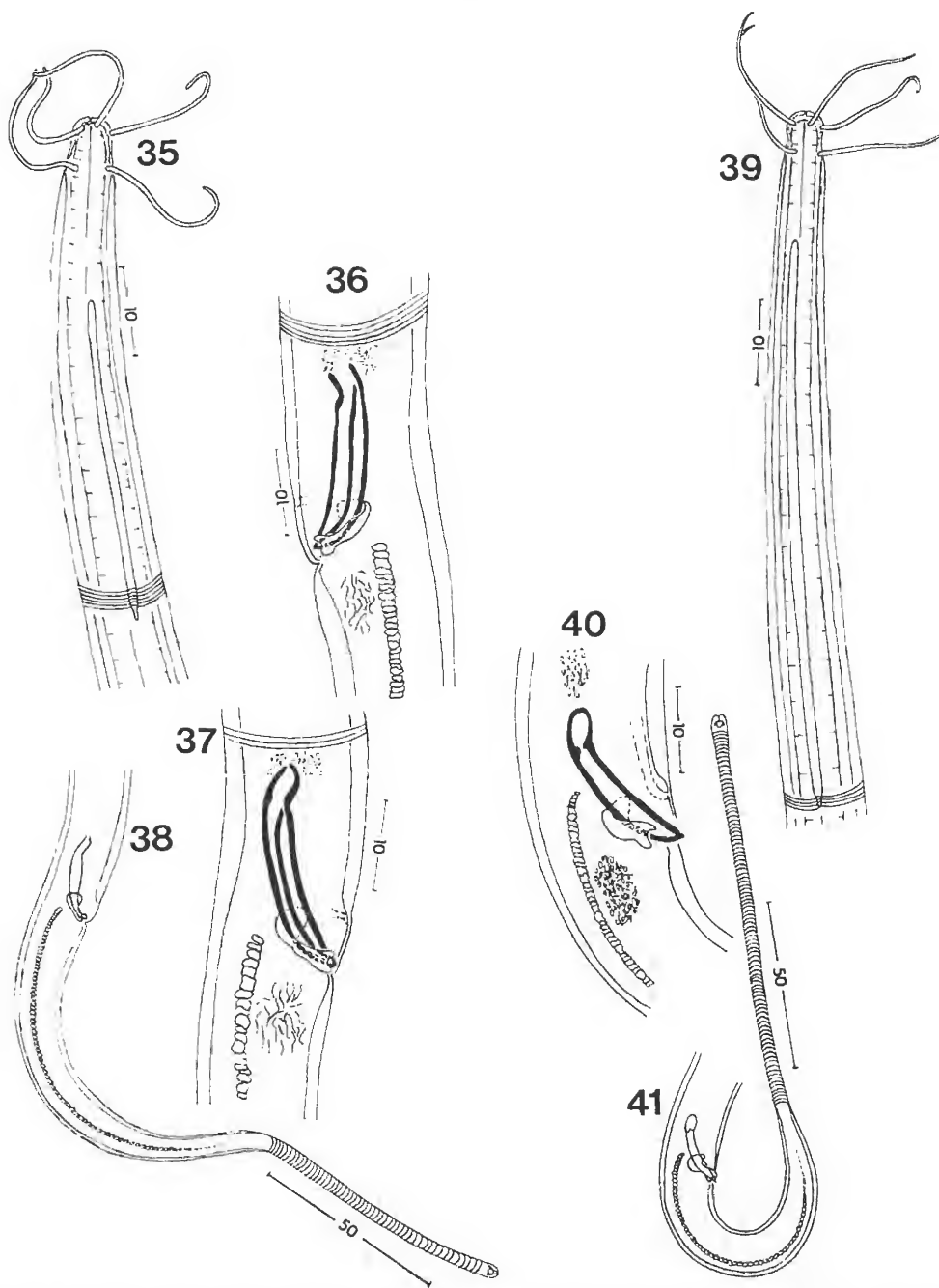
**Etymology:** From Latin *variabilis* meaning "to vary."

**Remarks:** *Halalaimus variabilis* n. sp. is the only species in Group 1 in which the males have ornamented caudal alae, a precloacal pore is present, a precloacal sensillum is absent, and inner labial sensilla are not discernible.

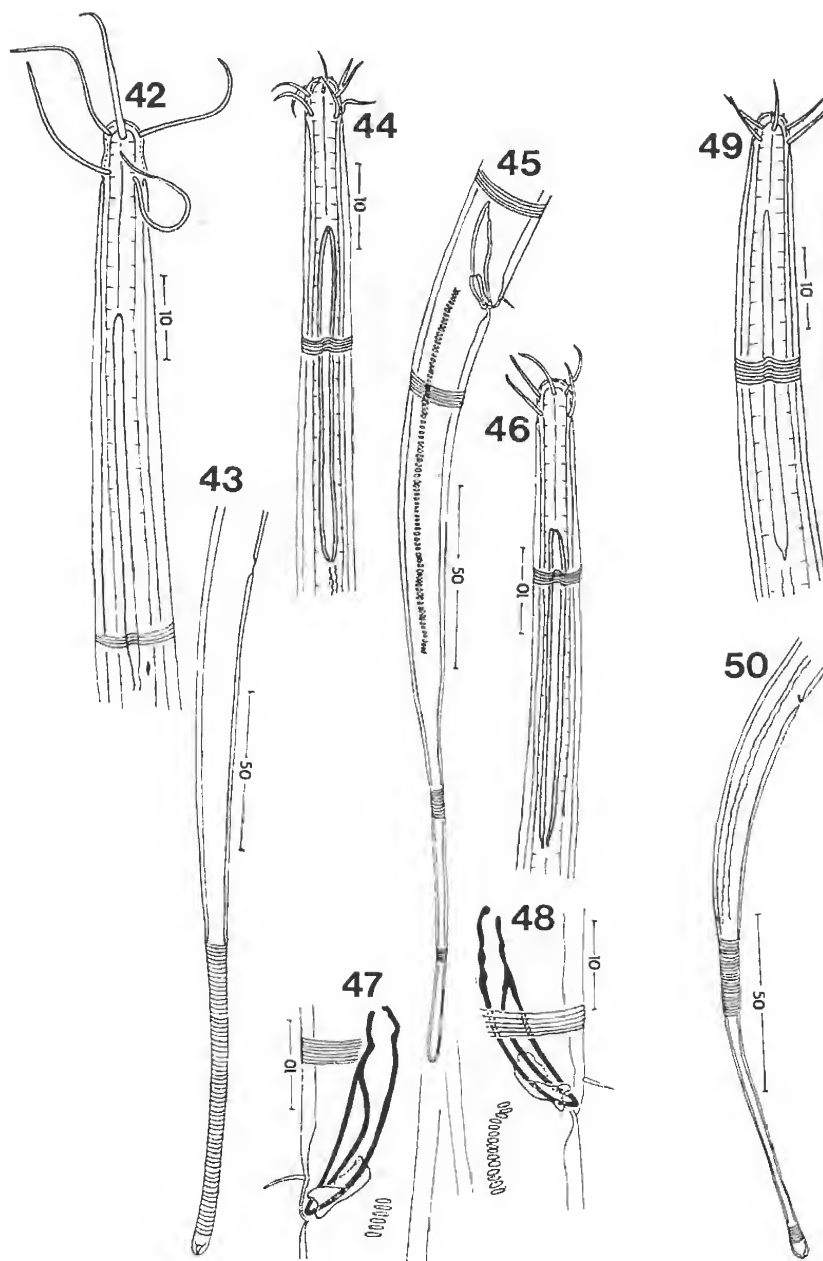
#### *Halalaimus paracomatus* n. sp.

Figs. 44-50

Cuticle with transverse striations, most evident posterior to nerve ring. Lateral alae present. Ornamented caudal alae present in male, unornamented caudal alae present in female. Inner labial sensilla papilliform. Outer labial and cephalic sensilla equal, in two circles close together. Male with setiform precloacal sensillum; precloacal pore absent. Excretory pore not observed. Conical part of tail without vermiculations in both sexes. Cylindrical part of tail with coarse transverse striations. Tail tip blunt, slightly bul-



Figs. 35-41. *Halalaimus variabilis* n. sp. Fig. 35. Male, anterior end, left lateral view. Fig. 36. Male number 1, cloacal region, left lateral view. Fig. 37. Male number 1, cloacal region, right lateral view. Fig. 38. Male number 3, posterior end, right lateral view. Fig. 39. Male, anterior end, right lateral view. Fig. 40. Male, cloacal region, right lateral view. Fig. 41. Male, posterior end, right lateral view. Scale bars in  $\mu\text{m}$ .



Figs. 42-43. *Halalaimus variabilis* n. sp. Fig. 42. Female, anterior end, right lateral view. Fig. 43. Female, posterior end, right lateral view. Figs. 44-50. *Halalaimus paracomatus* n. sp. Fig. 44. Male, anterior end, right lateral view. Fig. 45. Male, posterior end, right lateral view. Fig. 46. Male, anterior end, left lateral view. Fig. 47. Male, cloacal region, left lateral view. Fig. 48. Male, cloacal region, right lateral view. Fig. 49. Female, anterior end, right lateral view. Fig. 50. Female, posterior end, right lateral view. Scale bars in  $\mu\text{m}$ .

bous; spinneret present.

**Males (n = 2):** Length 1.41 mm (1.40-1.42). Width at midbody 24.5(24-25). Head diameter 4.2(4.2-4.2) at level of cephalic sensilla. Outer labial and cephalic sensilla 6.1(5.5-6.6) long. Labial surface to amphid 16.5(16-17) and nerve ring 252.5(251-254). Amphid 38(37-39) long. Esophagus 450.5(447-454) long. Tail 192(186-198) long. Width at cloaca 15.5(15-16). Spicules 24.5(24-25) long. Gubernaculum 9.5(9-10) long, consists of a plate with an extension lateral to each spicule tip; distal end cup-shaped; keel-like extension weakly developed.  $a = 57.6(56.8-58.3)$ ,  $b = 3.13(3.13-3.13)$ ,  $c = 7.35(7.07-7.63)$ .

**Female (n = 1):** Length 1.36 mm. Width at midbody 24. Head diameter 4.8 at level of cephalic sensilla. Outer labial and cephalic sensilla 6.4 long. Labial surface to amphid 13 and nerve ring 264. Amphid 44 long. Esophagus 473 long. Tail 181 long. Width at anus 11. Reproductive system amphidelphic; reflexed. Vulva 762 from anterior end.  $a = 56.7$ ,  $b = 2.88$ ,  $c = 7.51$ ,  $V = 56\%$ .

**Specimens:** Male holotype, USNM 77268; male paratype, USNM 77269.

**Locality:** St. Andrew Bay, Bay County, Florida (85° 40' 59" W, 30° 08' 23" N) and (85° 38' 52" W, 30° 07' 38" N). Water 7 meters and 11.1 meters deep.

**Etymology:** from Latin *para* meaning "near or beside" and *comatus* specific epithet for *Halalaimus comatus* Wieser, 1953.

**Remarks:** *Halalaimus paracomatus* n. sp. is very similar to *Halalaimus comatus* Wieser, 1953. *H. paracomatus* n. sp. differs from *H. comatus* in that the cylindrical part of the tail has coarse transverse striations, the tail tip does not have a spherical swelling, outer labial and cephalic sensilla are about equal in length, and the amphid is longer (5.3-8.8 versus 3.5 head diameters). *H. paracomatus* n. sp. is also similar to *Halalaimus americanus* n. sp. (described next) in the length of the outer labial and cephalic sensilla and absence of a spherical swelling at the tail tip. *H. paracomatus* n. sp. differs from *H. americanus* n. sp. in that the circles of outer labial and cephalic sensilla are closer together (0.67 versus 1.7-2.0 head diameters apart), the amphid is shorter (5.3-8.8 versus 19.3-20.3 head diameters), and the gubernaculum is rectangular without the distinct keel-like extension between the spicules that is present in *H. americanus* n. sp.

*Halalaimus americanus* n. sp.  
Figs. 51-59

Cuticle smooth, faint striations present at posterior end of lateral alae in one specimen. Broad lateral alae present, commencing at posterior end of amphid, fade into ornamented caudal alae in male. Inner labial sensilla not discernible. Outer labial and cephalic sensilla in two well-separated circles, unequal in length; outer labials shorter.

Excretory pore not observed. Precloacal sensillum present; precloacal pore absent. Conical part of tail with vermiculations. Cylindrical part of tail with coarse transverse striations. Tail tip blunt; spinneret present. Female unknown.

**Males (n = 3):** Length 1.45 mm (1.39-1.51). Width at midbody 23.3(22-24). Head diameter 3.1(3.0-3.2) at level of cephalic sensilla. Outer labial sensilla 3.5(3.0-4.4) long; cephalic sensilla 5.5(5.0-6.4) long. Labial surface to amphid 31(26-37) and nerve ring 246.5(235-258). Amphid 56.7(51-61) long. Esophagus 525.3(504-536) long. Tail 174(160-192) long. Width at cloaca 17(16-18). Spicules 26(24-27) long. Gubernaculum 8.5(8.0-9.6) long with narrow keel-like extension between spicules and extension lateral to each spicule; distal end of lateral extension cup-shaped. Cuticle on conical part of tail vermiculated.  $a = 62.3(60.8-63.2)$ ,  $b = 2.76(2.72-2.80)$ ,  $c = 8.40(7.86-8.69)$ .

**Specimens:** Holotype male, USNM 77270; paratype males, USNM 77506 & 77507.

**Locality:** St. Andrew Bay, Bay County, Florida, (85° 39' 07" W, 30° 08' 29" N) and (85° 39' 46" W, 30° 08' 40" N). Water 2.0 to 12.2 meters deep.

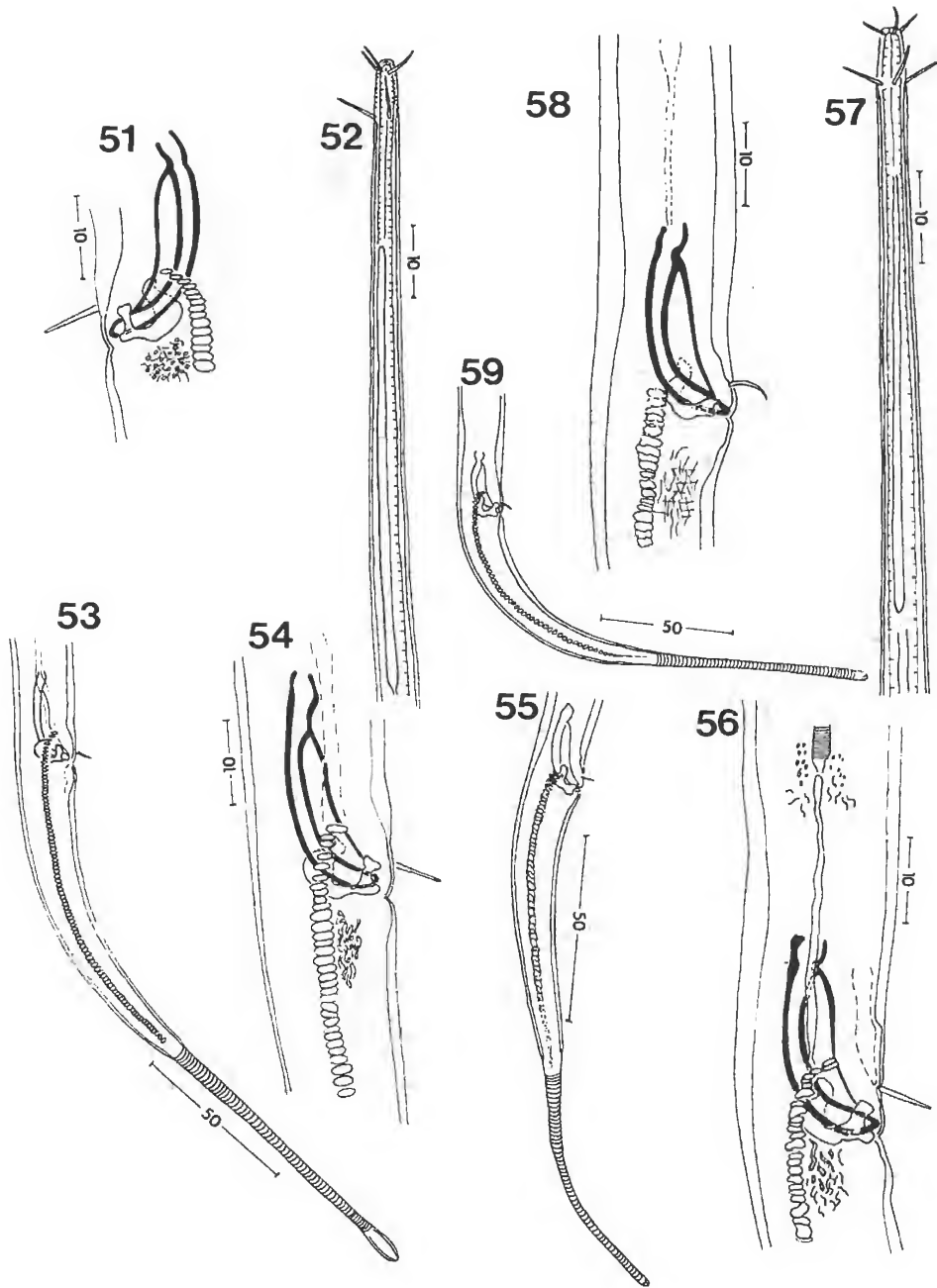
**Etymology:** Named after geographical location, America.

**Remarks:** *H. americanus* is similar to *H. paracomatus* n. sp. and differs from that species as discussed in the remarks section for *H. paracomatus* n. sp.

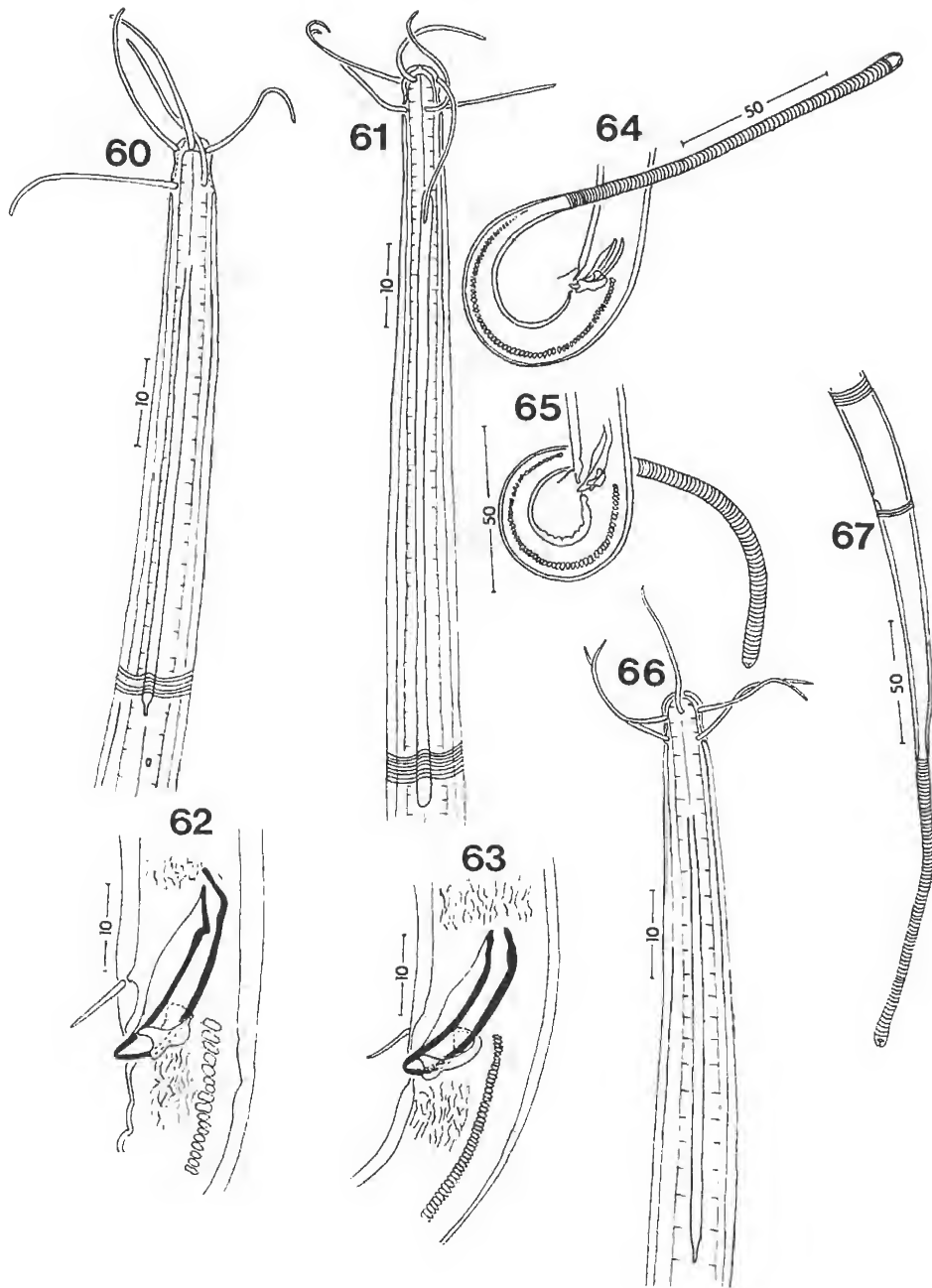
*Halalaimus floridanus* n. sp.  
Figs. 60-67

Cuticle faintly striated, appears punctate from midbody to precloacal region in male and anal region in female; cuticle of lateral fields also faintly vermiculated from midbody to cloacal region in male and anal region in female. Lateral alae not observed; ornamented caudal alae present in male; absent in female. Inner labial sensilla not discernible. Outer labial and cephalic sensilla equal in length. Lateral outer labial sensilla greater in diameter than other sensilla. Excretory pore not observed. Precloacal sensillum present and precloacal pore absent in male. Cuticle of conical part of tail vermiculated in male, not so in female. Cylindrical part of tail with coarse transverse striations. Tail tip blunt; spinneret present.

**Males (n = 4):** Length 1.53 mm (1.34-1.70). Width at midbody 18.5(16-21). Head diameter 4.4(4.0-4.8) at level of cephalic sensilla. Outer labial and cephalic sensilla 19.8(18-21) long. Labial surface to amphid 15.5(14-19) and nerve ring 202(192-208). Amphid 65.5(55-76) long. Esophagus 314.6(277-359) long. Tail 185.5(176-206) long. Width at cloaca 15(13-17). Spicules 20.8(18-24) long. Gubernaculum 8(8-8) long with small keel-like extension between spicules, and an extension lateral to each spicule tip; distal end of lateral extension cup-shaped.  $a = 82.7$



Figs. 51-59. *Halalaimus americanus* n.sp. Fig. 51. Male, cloacal region, left lateral view. Fig. 52. Male, anterior end, right lateral view. Fig. 53. Male, posterior end, right lateral view. Fig. 54. Male, cloacal region, right lateral view. Fig. 55. Male, posterior end, right lateral view. Fig. 56. Male, cloacal region, right lateral view. Fig. 57. Male, anterior end, right lateral view. Fig. 58. Male, cloacal region, right lateral view. Fig. 59. Male, posterior end, right lateral view. Scale bars in  $\mu\text{m}$ .



Figs. 60-67. *Halalaimus floridanus* n. sp. Fig. 60. Male, anterior end, left lateral view. Fig. 61. Male, anterior end, left lateral view. Fig. 62. Male, cloacal region, left lateral view. Fig. 63. Male, cloacal region, left lateral view. Fig. 64. Male posterior end, left lateral view. Fig. 65. Male, posterior end, left lateral view. Fig. 66. Female, anterior end, left lateral view. Fig. 67. Female, posterior end, left lateral view. Scale bars in  $\mu\text{m}$ .

(74.4-89.5).  $b = 4.86(4.67-5.13)$ .  $c = 8.22(7.61-9.16)$ .

**Female (n = 1):** Length 1.58 mm. Width at midbody 27. Head diameter 4.8 at level of cephalic sensilla. Outer labial and cephalic sensilla 16 long. Labial surface to amphid 15 and nerve ring 194. Amphid 54 long. Esophagus 321 long. Width at anus 15. Tail 227 long. Anterior to vulva 884. Reproductive system amphidelphic; reflexed.  $a = 58.5$ .  $b = 4.92$ .  $c = 11.4$ .  $V = 53\%$ .

**Specimens:** Male holotype, USNM 77271; male paratypes, USNM 77272-77275; female allotype, USNM 77276.

**Locality:** Mouth of Freshwater Bayou off St. Andrew

Bay, Bay County, Florida (85° 39'00"W, 30° 07'30"N). Water 1.0 meter deep. Two male paratypes from Biscayne Bay, Dade County, Florida provided by Dr. Tarjan.

**Etymology:** Named for the geographic locality, state of Florida.

**Remarks:** *Halalaimus floridanus* n. sp. is the only species in group 1 with the following combination of characters: cylindrical part of tail with coarse transverse striations, precloacal sensillum present, precloacal pore absent, and the outer labial and cephalic sensilla are 4.4 head diameters long or longer.

**Artificial Key to the Males of Group 1**  
(HD = head diameter; CD = cloacal diameter)

1. Cervical, somatic, and caudal sensilla present ..... *Halalaimus thalassinus* n. sp.  
Cervical, somatic, and caudal sensilla absent ..... 2
- 2(1). Precloacal pore present; precloacal sensillum absent ..... 3  
Precloacal pore absent; precloacal sensillum present ..... 4
- 3(2). Precloacal pore with large glandular structure; outer labial and cephalic sensilla 1.0 HD long .....  
..... *Halalaimus sobakini* Sergeeva, 1973  
Precloacal pore without large glandular structure; outer labial and cephalic sensilla 3.3 HD long .....  
..... *Halalaimus variabilis* n. sp.
- 4(2). Cylindrical part of tail with coarse transverse striations ..... 5  
Cylindrical part of tail without coarse transverse striations ..... 9
- 5(4). Outer labial and cephalic sensilla equal to or greater than 3.0 HD long ..... 6  
Outer labial and cephalic sensilla less than or equal to 2.0 HD long ..... 7
- 6(5). Outer labial and cephalic sensilla 3.0 HD long; inner labial sensilla discernible; amphid begins 7.0 HD from anterior end ..... *Halalaimus bayensis* n. sp.  
Outer labial and cephalic sensilla 4.5 HD long; inner labial sensilla not discernible; amphid begins 3.5 HD from anterior end ..... *Halalaimus floridanus* n. sp.
- 7(5). Outer labial and cephalic sensilla in two well-separated circles, 1.0-1.8 HD apart; outer labial sensilla shorter than cephalic sensilla ..... 8  
Outer labial and cephalic sensilla in two circles close together, 0.43-0.50 HD apart; outer labial and cephalic sensilla equal in length ..... *Halalaimus paracomatus* n. sp.
- 8(7). Broad lateral somatic alae present; spicules 1.5 CD long; amphid narrow, 17-19 HD long; inner labial sensilla not discernible ..... *Halalaimus americanus* n. sp.  
Broad lateral somatic alae absent; spicules 2.0-2.1 CD long; amphid broad, 7.5-8.6 HD long; inner labial sensilla discernible ..... *Halalaimus tarjani* n. sp.
- 9(4). Outer labial and cephalic sensilla in two well-separated circles, 1.2 HD apart; inner labial sensilla discernible ..... *Halalaimus bulbocaudatus* n. sp.  
Outer labial and cephalic sensilla in two circles close together, 0.2 HD apart; inner labial sensilla not discernible ..... *Halalaimus comatus* Wieser, 1953

### Group 2

Males of the species in this group have caudal alae that are ornamented or unornamented. Precloacal sensillum and precloacal pore absent. Inner labial sensilla discernible in some species. Outer labial and cephalic sensilla of varying length between circles. Circles of sensilla varying distances apart.

Cylindrical part of tail with or without coarse transverse striations. Tail tip blunt, bifurcate, or flagellate.

#### *Halalaimus gracilis* De Man, 1888

*Halalaimus gracilis* has been reported from a number of localities world-wide and various descriptions have been published. De Man (1888) described *H. gracilis* on the basis of a male and a female from the North Sea. A circle of setiform inner labial sensilla is present in addition to the circles of outer labial and cephalic sensilla. The male has ornamented caudal alae, and a setiform precloacal sensillum and pore are absent. The gubernaculum is figured as a narrow plate without an apophysis or lateral extensions. De Man (1922) described additional specimens of *H. gracilis*.

Stekhoven (1935) described specimens of a species of *Halalaimus* as *H. gracilis*, but did not mention or figure the presence of the ornamented caudal alae. In the absence of this information, *H. gracilis* sensu Stekhoven (1935) is considered a species inquirenda. Stekhoven (1935) also placed *Halalaimus droebachiensis* Allgen, 1931 as a synonym of *H. gracilis* sensu Stekhoven (1935). The description given by Allgen (1931) was based on a female specimen and does not mention or figure the inner labial sensilla present in *H. gracilis*. Therefore, this species is also considered to be a species inquirenda.

Bresslau and Stekhoven (1940) described specimens of a species of *Halalaimus* as *H. gracilis* but did not describe or figure the ornamented caudal alae or inner labial sensilla characteristic of *H. gracilis*. These specimens appear similar to those described by Stekhoven (1935) and are, therefore, considered to be a species inquirenda. Stekhoven (1950) described what he considered to be a female of *H. gracilis*. Inner labial sensilla are not described, but the figure indicates that they may be present. In view of the doubt as to the presence or absence of inner labial sensilla, the specimen is considered a species inquirenda.

Timn (1952) described a male specimen of a species of *Halalaimus* that he referred to as *H. gracilis*. However, he did not describe or figure the presence of inner labial sensilla and did not mention or figure the presence or absence of ornamented caudal alae. Timn (1952) did state that the specimen had a smooth cuticle and lateral alae were absent. In view of the absence of information and figures,

*H. gracilis* sensu Timm, 1952 is also considered to be a species inquirenda.

#### *Halalaimus gerlachi* n. sp.

Synonym: *Halalaimus gracilis* sensu Gerlach, 1967; nec *H. gracilis* De Man, 1888.

Gerlach (1967) described specimens of *Halalaimus* from the Red Sea as *H. gracilis*. Inner labial sensilla are not discernible and lateral alae are present in the specimens. Males have ornamented caudal alae, and the gubernaculum has a caudally directed apophysis. The absence of the inner labial sensilla and the presence of a gubernacular apophysis is sufficient to differentiate the specimens from *H. gracilis* and designate them as a new species, *Halalaimus gerlachi* n. sp. (Gerlach 1967). The holotype of the species is the specimen on which Gerlach (1967) based his description. The only other species of *Halalaimus* with a gubernaculum with an apophysis is *Halalaimus sarsi* Gerlach, 1967. *H. gerlachi* n. sp. differs from *H. sarsi* in the presence of ornamented caudal alae and shorter outer labial and cephalic sensilla (1.5 versus 2.0 head diameters long).

Platt and Warwick (1983) described specimens of *Halalaimus* as *H. gracilis*. The inner labial sensilla are not mentioned or figured, caudal alae are absent in the male, and a precloacal sensillum is present. Based on the description, these specimens cannot be *H. gracilis*. They belong in group 3 below along with those species in which a precloacal sensillum is present and caudal alae are absent.

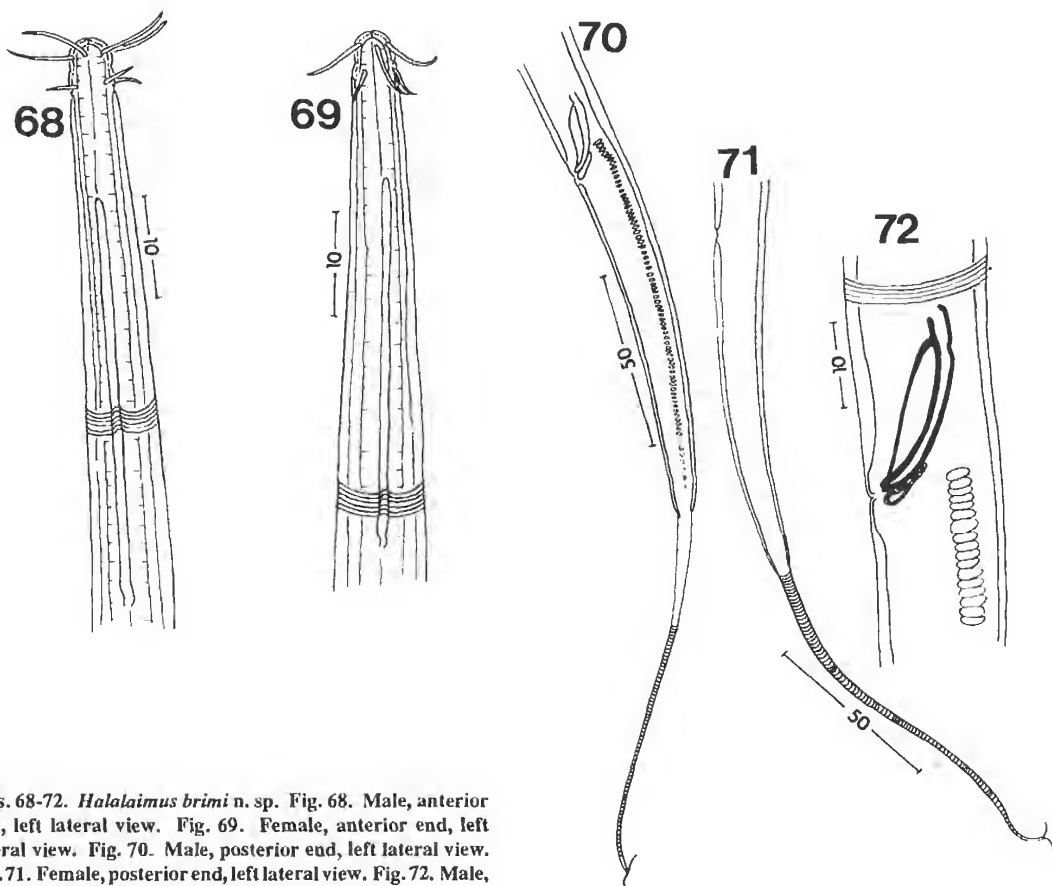
#### *Halalaimus brimi* n. sp.

Figs. 68-72

Cuticle with transverse striations. Lateral alae not observed. Ornamented caudal alae present in male; caudal alae absent in female. Inner labial sensilla not discernible. Outer labial sensilla longer than cephalic sensilla; circles far apart. Excretory pore not observed. Precloacal sensillum and pore absent. Conical part of tail without vermiculations; cylindrical part of tail with coarse transverse striations. Tail tip bifurcate.

**Male (n = 1):** Length 1.27 mm. Width at midbody 22. Head diameter 4.7 at level of cephalic sensilla. Outer labial sensilla 7.0 long. Cephalic sensilla 3.3 long. Labial surface to amphid 16 and nerve ring 203. Amphid 41 long. Esophagus 328 long. Width at cloaca 16. Tail 192 long. Spicules 23 long. Gubernaculum 6.8 long, expanded distally, narrowed proximally. a = 57.7. b = 3.87. c = 6.61.

**Female (n = 2):** Length 1.31 mm (1.30-1.32). Width at midbody 26(25-27). Head diameter 4.6(4.5-4.7) at level of cephalic sensilla. Outer labial sensilla 6.3(6.3-6.3) long. Cephalic sensilla 3.3(3.3-3.3) long. Labial surface to amphid 14.5(14-15) and nerve ring 198(191-205). Amphid 36(35-37) long. Esophagus 360(359-361) long. Width at



Figs. 68-72. *Halalaimus brimi* n. sp. Fig. 68. Male, anterior end, left lateral view. Fig. 69. Female, anterior end, left lateral view. Fig. 70. Male, posterior end, left lateral view. Fig. 71. Female, posterior end, left lateral view. Fig. 72. Male, cloacal region, left lateral view. Scale bars in  $\mu\text{m}$ .

anus 14(14-14). Tail 198(196-200) long. Vulva 681(674-688) from anterior end. Reproductive system amphidelphic; reflexed.  $a = 50.3(48.1-52.4)$ .  $b = 3.63(3.62-3.64)$ .  $c = 6.58(6.50-6.65)$ .  $V = 52.5\%(52-53)$ .

**Specimens:** Male, holotype, USNM 77277; female allotype, USNM 77278; female paratype, USNM 77509.

**Locality:** St. Andrew Bay, Bay County, Florida ( $85^{\circ} 38' 52''\text{W}$ ,  $30^{\circ} 07' 38''\text{N}$ ). Water 8.0 meters deep.

**Etymology:** Named for Mr. Michael Brim of the United States Fish and Wildlife Service, Panama City, Florida without whose support many of the specimens included in this study would not have been obtained.

**Remarks:** *Halalaimus brimi* n. sp. is the only species in this group with a bifurcate tail tip and with outer labial

sensilla longer than cephalic sensilla. *H. brimi* n. sp. is similar to *Halalaimus diacros* Mawson, 1958 in the presence of a bifurcate tail. *H. brimi* n. sp. differs from *H. diacros* in the presence of ornamented caudal alae and the presence of outer labial sensilla that are longer than the cephalic sensilla. *H. brimi* n. sp. is also similar to *Halalaimus horridus* Gerlach, 1956 in that the outer labial sensilla are longer than the cephalic sensilla. *H. brimi* n. sp. differs from *H. horridus* in the shorter length of the labial and cephalic sensilla (1.3-1.5 and 0.7 versus 3.0 and 1.0 head diameters long), in the presence of a bifurcate tail tip, and in the presence of coarse transverse striations on the cylindrical part of the tail.

**Artificial Key to the Males of Group 2**  
(HD = head diameter; CD = cloacal diameter)

1. Caudal alae unornamented ..... 2  
Caudal alae ornamented ..... 7
- 2(1). Inner labial sensilla discernible ..... *Halalaimus alatus* Timm, 1952  
Inner labial sensilla not discernible ..... 3
- 3(2). Tail flagellate 30-42 CD long ..... 4  
Tail not flagellate 8-16 CD long ..... 5
- 4(3). Tail 30 CD long; outer labial and cephalic sensilla 1.7 HD long, in two circles 0.2 HD apart .....  
..... *Halalaimus relatatus* Gerlach, 1967  
Tail 42 CD long; outer labial and cephalic sensilla 1.2 HD long, in two circles 1.0 HD apart .....  
..... *Halalaimus filum* Gerlach, 1962
- 5(3). Gubernaculum with dorso-caudally directed apophysis ..... *Halalaimus sarsi* Gerlach, 1967  
Gubernaculum without dorso-caudally directed apophysis ..... 6
- 6(5). Outer labial sensilla papilliform; cephalic sensilla 0.33 HD long; "a" = 58.5 .....  
..... *Halalaimus lineatoides* Timm, 1961  
Outer labial and cephalic sensilla setiform, 1.0 HD long; "a" = 100.0 .....  
..... *Halalaimus lineatus* Timm, 1961
- 7(1). Tail tip bifurcate ..... *Halalaimus brimi* n. sp.  
Tail tip not bifurcate ..... 8
- 8(7). Gubernaculum with dorso-caudally directed apophysis; inner labial sensilla not discernible .....  
..... *Halalaimus gerlachi* n. sp.  
Gubernaculum without dorso-caudally directed apophysis; inner labial sensilla discernible .....  
..... *Halalaimus gracilis* De Man, 1888

**Group 3**

Males without caudal alae. Precloacal sensillum and/or precloacal pore present. Inner labial sensilla discernible in some species, not so in others. Outer labial and cephalic sensilla can vary in length between circles. Circles of varying distances apart. Cylindrical part of tail with or without coarse transverse striations. Tail tip blunt, bifurcate, or flagellate.

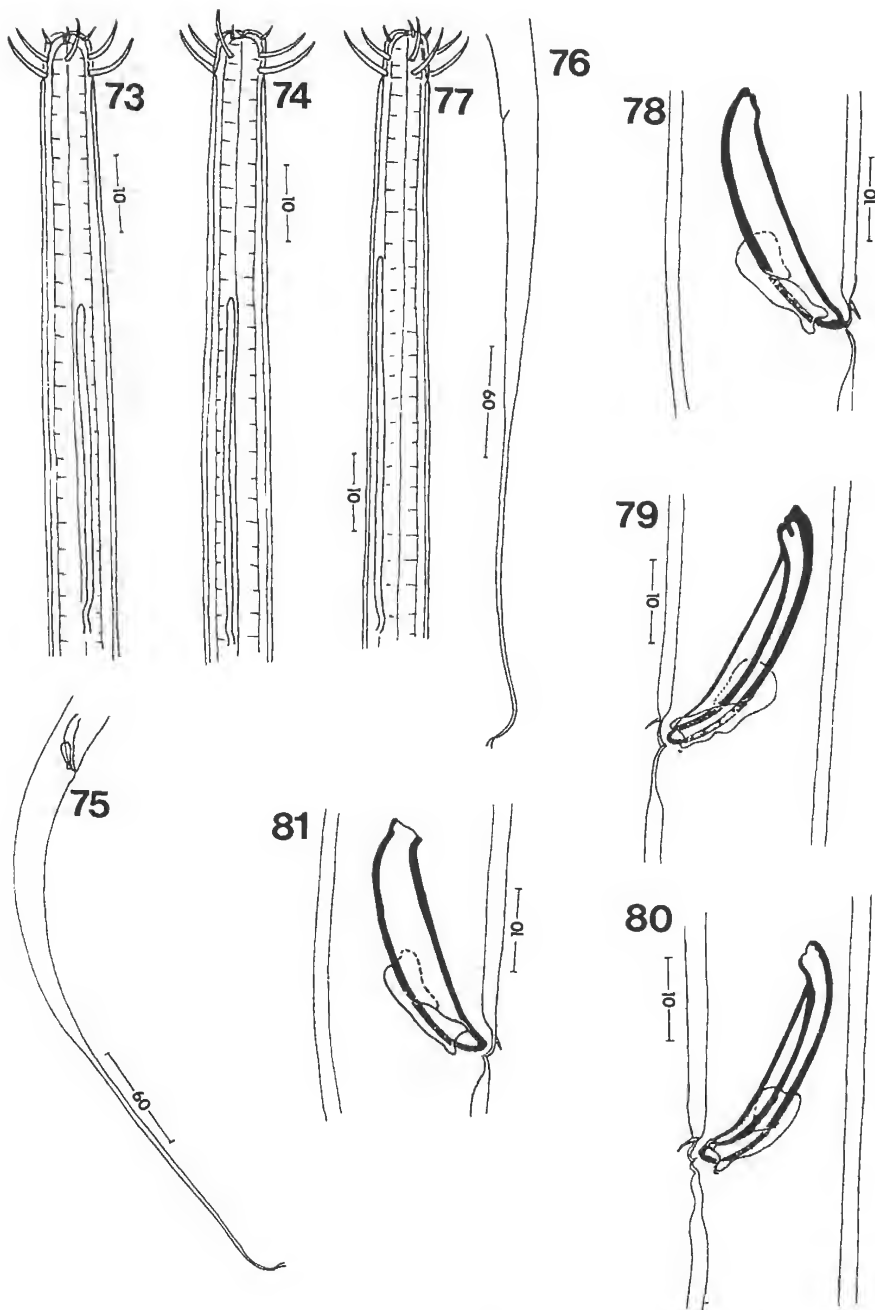
***Halalaimus paraletcheri* n. sp.**  
**Figs. 73-81**

Cuticle smooth. Lateral and caudal alae not observed. Inner labial sensilla setiform. Outer labial sensilla shorter than cephalic sensilla. Excretory pore not observed. Small precloacal sensillum present, precloacal pore absent in

males. Conical part of tail without vermiculations; cylindrical part of tail without coarse transverse striations. Tail tip bifurcate.

**Males (n = 3):** Length 2.29 mm (2.17-2.44). Width at midbody 34(32-35). Head diameter 6.4(6.4-6.4) at level of cephalic sensilla. Inner labial sensilla 2.6(2.4-3.0) long. Outer labial sensilla 6.1(5.6-6.4) long. Cephalic sensilla 7.7(7.2-8.0) long. Labial surface to amphid 35.3(34-37) and nerve ring 449(432-459). Amphid 42.3(40-45) long. Esophagus 628(605-649) long. Width at cloaca 21.7(21-22). Tail 320(304-336) long. Spicules 32(32-32) long; right spicule broader than left. Gubernaculum 16(16-16) long with keel-like extension between spicules and extensions lateral to spicule, distal end of each lateral extension cup-shaped. a = 67.5(62.0-70.9). b = 3.65(3.59-3.76). c = 7.18(6.76-7.63).

**Females (n = 2):** Length 2.53 mm (2.27-2.78). Width at midbody 45.5(43-48). Head diameter 6.4(6.4-6.4) at



Figs. 73-81. *Halalaimus paraftletcheri* n. sp. Fig. 73. Male, anterior end, right lateral view. Fig. 74. Male, anterior end, left lateral view. Fig. 75. Male, posterior end, right lateral view. Fig. 76. Female, posterior end, left lateral view. Fig. 77. Female, anterior end, left lateral view. Fig. 78. Male, cloacal region, right lateral view. Fig. 79. Male, cloacal region, left lateral view. Fig. 80. Male, cloacal region, right lateral view. Fig. 81. Male, cloacal region, left lateral view. Scale bars in µm.



## Group 4

Males without caudal alae. Precloacal sensillum and precloacal pore absent. Inner labial sensilla discernible in some species, in other species not so. Outer labial and cephalic sensilla can vary in length between circles. Circles

varying distances apart. Cylindrical part of tail with or without coarse transverse striations. Tail tip blunt, bifurcate or flagellate. Single specimens of *Halalaimus* species belonging to this group were examined but are not included in the following key or described.

**Artificial Key to the Males of Group 4**  
(HD = head diameter; CD = cloacal diameter)

1. Outer labial and cephalic sensilla in two circles of 6 and 6 ..... 2  
Outer labial and cephalic sensilla in two circles of 6 and 4 ..... 3
- 2(1). Tail tip bifurcate ..... *Halalaimus filicollis* Timm, 1961  
Tail tip not bifurcate ..... *Halalaimus setosus* Timm, 1961
- 3(1). Cuticle with coarse longitudinal striations ..... *Halalaimus longistriatus* Timm, 1961  
Cuticle without coarse longitudinal striations ..... 4
- 4(3). Tail tip bifurcate ..... 5  
Tail tip not bifurcate ..... 6
- 5(4). Cylindrical part of tail with coarse transverse striations ..... *Halalaimus diacros* Mawson, 1958  
Cylindrical part of tail without coarse transverse striations ..... *Halalaimus fletcheri* Mawson, 1958
- 6(4). Cylindrical part of tail with coarse transverse striations ..... 7  
Cylindrical part of tail without coarse transverse striations ..... 9
- 7(6). Amphid width 23-36% of corresponding body diameter ..... *Halalaimus pachydoroides* Vitiello, 1970  
Amphid width 10-16% of corresponding body diameter ..... 8
- 8(7). Gubernaculum present ..... *Halalaimus filicorpus* Vitiello, 1970  
Gubernaculum absent ..... *Halalaimus turbidus* Vitiello, 1970
- 9(6). Cephalic sensilla equal to or greater than 4.0 HD long ..... 10  
Cephalic sensilla less than or equal to 2.2 HD long ..... 13
- 10(9). Tail 44.6 CD long ..... *Halalaimus meyersi* Wieser & Hopper, 1967  
Tail equal to or less than 20.4 CD long ..... 11
- 11(10). Outer labial sensilla shorter (2.1 HD long) than cephalic sensilla (4.0 HD long) .....  
..... *Halalaimus floescens* Gerlach, 1967  
Outer labial and cephalic sensilla equal, 4.0-6.0 HD long ..... 12
- 12(11). Circles of outer labial and cephalic sensilla well-separated (2.2-2.6 HD apart); gubernaculum without ventral curve ..... *Halalaimus supercirrhatus* Gerlach, 1955  
Circles of outer labial and cephalic sensilla closer together (1.0 HD apart); gubernaculum with ventral curve ..... *Halalaimus capitulatus* Boucher, 1977
- 13(9). Inner labial sensilla discernible ..... *Halalaimus papillifer* Gerlach, 1956  
Inner labial sensilla not discernible ..... 14

|         |  |    |
|---------|--|----|
| 14(13). | Cuticle with transverse striations . . . . .   | 15 |
|         | Cuticle without transverse striations . . . . .  | 18 |
| 15(14). | Tail filiform, 17.7-24.5 CD long, tip pointed . . . . .  | 16 |
|         | Tail not filiform, 8.3-15.0 CD long, tip pointed or blunt . . . . .  | 17 |
| 16(15). | Amphid 23 HD long; circles of outer labial and cephalic sensilla close together (0.33 HD apart)<br><i>Halalaimus lutarus</i> Vitiello, 1970<br>Amphid 8.6 HD long; circles of outer labial and cephalic sensilla far apart (1.0 HD apart)<br><i>Halalaimus longicollis</i> Allg n, 1932  |    |
| 17(15). | Tail 8.3 CD long, tip pointed . . . . . <i>Halalaimus macquariensis</i> Mawson, 1958<br>Tail 10.5-15.0 CD long, tip blunt . . . . . <i>Halalaimus longicaudatus</i> Filipjev, 1927   |    |
| 18(14). | Gubernaculum absent or rudimentary . . . . .   | 19 |
|         | Gubernaculum present, well developed . . . . .   | 20 |
| 19(18). | Gubernaculum absent . . . . . <i>Halalaimus rectispiculatus</i> Platonova, 1971<br>Gubernaculum rudimentary, a small plate at distal end of spicules . . . . .<br><i>Halalaimus leptoderma</i> Platonova, 1971   |    |
| 20(18). | "a" = 217.7 . . . . . <i>Halalaimus leptosoma</i> Southern, 1914<br>"a" = 130.0 or less . . . . .  | 21 |
| 21(20). | Tail tip pointed . . . . .   | 22 |
|         | Tail tip blunt . . . . .   | 23 |
| 22(21). | Outer labial and cephalic sensilla 1.7 HD long, in two circles close together . . . . .<br><i>Halalaimus anne</i> Sergeeva, 1972<br>Outer labial and cephalic sensilla 0.2 HD long, in two well-separated circles . . . . .<br><i>Halalaimus ciliocaudatus</i> Allg n, 1932  |    |
| 23(21). | Cylindrical part of tail 12% of total tail length . . . . . <i>Halalaimus pachyderma</i> Filipjev, 1927<br>Cylindrical part of tail 25% or more of total tail length . . . . .   | 24 |
| 24(23). | Outer labial and cephalic sensilla less than 1.0 HD long . . . . .   | 25 |
|         | Outer labial and cephalic sensilla greater than 1.0 HD long . . . . .  | 26 |
| 25(24). | Circles of outer labial and cephalic sensilla 1.7 HD apart; amphid 8.6 HD from anterior end; distal end of<br>gubernaculum expanded laterally . . . . . <i>Halalaimus zenkevitchi</i> Filipjev, 1927<br>Circles of outer labial and cephalic sensilla 0.78 HD apart; amphid 2.2-4.6 HD from anterior end; distal end<br>of gubernaculum not expanded laterally . . . . . <i>Halalaimus isaitshikovi</i> Filipjev, 1927 |    |
| 26(24). | Circles of outer labial and cephalic sensilla 1.0 HD apart . . . . . <i>Halalaimus parvus</i> Chitwood, 1936<br>Circles of outer labial and cephalic sensilla 0.5 HD or less apart . . . . .   | 27 |
| 27(26). | "c" = 15.9 . . . . . <i>Halalainius brevispiculum</i> Sergeeva, 1973<br>"c" = 9.0 or less . . . . .  | 28 |
| 28(27). | Amphid 5.6 HD from anterior end, 9.2 HD long . . . . . <i>Halalaimus wodjanizkii</i> Sergeeva, 1972<br>Amphid 3.0-3.2 HD from anterior end, 6.0-12.0 HD long . . . . .   | 29 |
| 29(28). | Amphid 6.0 HD long; gubernaculum without lateral extensions . . . . .<br><i>Halalaimus caroliniensis</i> Chitwood, 1936<br>Amphid 12.0 HD long; gubernaculum with lateral extensions . . . . .<br><i>Halalaimus jaltensis</i> Sergeeva, 1973   |    |

The construction of a key to the females of the species of *Halalaimus* is more difficult than for males. Characters are not as distinct and many descriptions are not sufficiently complete to separate individual species. The following key ends with groups of similar species that could

not be easily separated. Females are not known for a number of species. The following species were not included due to the absence of necessary information; *Halalaimus leptoderma* Platonova, 1971 and *Halalaimus leptosoma* Southern, 1914.

**Artificial Key to the Females of the Genus *Halalaimus***  
(HD = head diameter, AD = anal diameter)

1.     Outer labial and cephalic sensilla in two circles of 6 + 6 ..... 2  
        Outer labial and cephalic sensilla in two circles of 6 + 4 ..... 3
- 2(1).   Tail tip bifurcate ..... *Halalaimus filicollis* Timm, 1961  
        Tail tip not bifurcate ..... *Halalaimus setosus* Timm, 1961
- 3(1).   Cuticle with coarse longitudinal striations ..... *Halalaimus longistriatus* Timm, 1961  
        Cuticle without coarse longitudinal striations ..... 4
- 4(3).   Tail tip bifurcate ..... 5  
        Tail tip not bifurcate ..... 8
- 5(4).   Cylindrical part of tail with coarse striations ..... 6  
        Cylindrical part of tail without coarse striations ..... 7
- 6(5).   Outer labial sensilla twice length of cephalic sensilla ..... *Halalaimus brimi* n. sp.  
        Outer labial and cephalic sensilla equal ..... *Halalaimus diacros* Mawson, 1958
- 7(5).   Circles of outer labial and cephalic sensilla well-separated (0.73-0.83 HD apart) .....  
        ..... *Halalaimus fletcheri* Mawson, 1958  
        Circles of outer labial and cephalic sensilla close together (0.30-0.38 HD apart) .....  
        ..... *Halalaimus parafrletcheri* n. sp.
- 8(4).   Cervical and caudal sensilla present ..... 9  
        Cervical and caudal sensilla absent ..... 10
- 9(8).   Lateral alae present; outer labial and cephalic sensilla equal; inner labial sensilla papilliform .....  
        ..... *Halalaimus thalassinus* n. sp.  
        Lateral alae absent; outer labial sensilla shorter than cephalic sensilla; inner labial sensilla not discernible  
        ..... *Halalaimus delamarei* Vitiello, 1970
- 10(8).  Tail tip a spherical bulb ..... 11  
        Tail tip not a bulb ..... 13
- 11(10). Circles of outer labial and cephalic sensilla well-separated (1.0 HD apart); inner labial sensilla papilliform  
        ..... *Halalaimus bulbocaudatus* n. sp.  
        Circles of outer labial and cephalic sensilla well-separated or not; inner labial sensilla not discernible ..  
        ..... 12
- 12(11). Circles of outer labial and cephalic sensilla well-separated (greater than 1.0 HD apart) .....  
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Isopods of the Genus *Excorallana* Stebbing, 1904 (Crustacea, Isopoda, Corallanidae) from the East Coast of Mexico with a Supplemental Description of *E. subtilis*

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## ISOPODS OF THE GENUS *EXCORALLANA* STEBBING, 1904 (CRUSTACEA, ISOPODA, CORALLANIDAE) FROM THE EAST COAST OF MEXICO WITH A SUPPLEMENTAL DESCRIPTION OF *E. SUBTILIS*

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**ABSTRACT** Eight species of *Excorallana*, *E. acuticauda*, *E. delaneyi*, *E. oculata*, *E. sexticornis*, *E. subtilis*, *E. tricornis*, *E. warmingii*, and *Excorallana* sp. are recorded for the eastern coast of Mexico. The range of *E. delaneyi* is extended south in the Gulf of Mexico. *Excorallana oculata* and *E. subtilis* are reported for the first time in the Gulf. Based on specimens from the east coast of Mexico, a supplemental description of *E. subtilis* is presented and its taxonomy to other closely related species discussed. A key is provided to the adult males of the species of *Excorallana* now known to occur in the southwestern Gulf of Mexico and the Caribbean coast of Mexico.

### INTRODUCTION

A variety of marine isopod crustaceans have been collected in conjunction with ongoing ecological and faunal surveys off the eastern coast of Mexico. This study deals with the new distribution records for the excorallanid isopod genus *Excorallana* Stebbing, 1904 from the Gulf and the Caribbean coasts of Mexico. Except for *E. oculata*, which occurs in both the eastern (west coast of Africa) and the western Atlantic, the 21 other species of *Excorallana* are restricted to the tropical and temperate waters of the Atlantic and Pacific coasts of the Americas. Of these, 16 species are endemic to the western Atlantic between 30°N and the Equator (Lemos de Castro and Lima 1971; Delaney 1989). The range of *E. delaneyi* is extended south in the Gulf. *Excorallana oculata* and *E. subtilis* are reported for the first time in the Gulf. Six female specimens of the latter species were collected in Sabancuy, Campeche and Puerto Morelos, Quintana Roo, allowing its redescription and the determination of differences among the specimens reported from Brazil by Lemos de Castro and Lima in 1971.

### MATERIALS AND METHODS

Specimens used for this study were obtained from several localities and sites along the eastern coast of Mexico (Fig. 1). These were Isla de Sacrificios off Veracruz, Sabancuy and El Cayo in Terminos Lagoon; Seibaplaya, Campeche; Yucalpetén and Río Lagartos, Yucatán, Isla Mujeres, and along the shore and the barrier reef off Puerto

Morelos in the Yucatan Peninsula. Specimens from Terminos Lagoon were collected during 1983 in seagrass beds (*Thalassia testudinum*) using a 0.65m wide (0.451mm mesh) Colman-Segrove sled (Eleftheriou and Holme 1985). Other specimens were obtained from hand-collected sponges living on the seagrass beds at El Cayo. Material from the Yucatán Peninsula and Sacrificios Island was hand-collected while skin diving and SCUBA diving during several field trips from 1985 to 1987.

The specimens examined during this study are deposited in the Carcinological Collection at the Instituto de Biología, National University of Mexico (IB-UNAM). Water temperature was recorded in the field with a hand thermometer. The four to five digit catalogue numbers for these specimens are preceded by the letters EM. Specimens were fixed in 10% seawater formalin, sorted in the laboratory, identified, catalogued, and stored in 70% ethanol. The sex, total length (L) and width (W) of each specimen is indicated under material examined for each species. The length and width were determined using a calibrated ocular micrometer in a dissecting microscope. Illustrations were made with the aid of a camera lucida.

### RESULTS

Eight species of *Excorallana* taken along the coast of eastern Mexico have been identified in the collections of IB-UNAM. Specific information on the occurrence, habitat, and hosts, when known, is presented for each species treated.

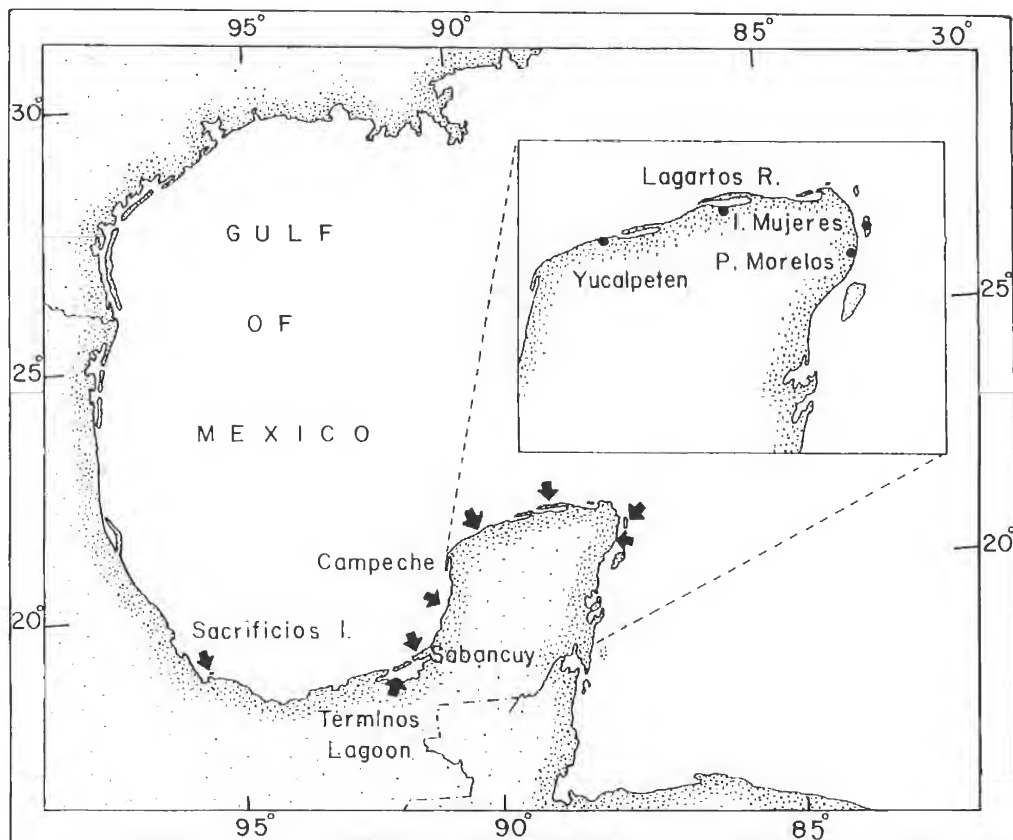


Figure 1. Sampling sites of *Excorallana* specimens recorded in this study in the southwestern Gulf of Mexico and the Mexican Caribbean.

*Excorallana acuticauda* (Miers 1881)

Fig. 2 a-c

**Material examined.** Puerto Morelos; EM-9588 f L:6.6, W:2.0mm.

**Diagnosis.** Eyes large, not contiguous, separated by a distance of half the length of an eye. Males and females without cephalic horns. Telson with lateral notches and mid-dorsal excavation. Frontal lamina elongate, distal end round.

**Distribution.** Key West, Florida; St. Thomas (Richardson 1905); South Bank, Texas (Clark and Robertson 1982); Caribbean and Brazil (Delaney 1989). New record: Puerto Morelos, Quintana Roo, Mexico.

**Ecological notes:** Occurs in reefs, low tide (Richardson 1905). Intertidal (Schultz 1969). At Puerto Morelos, associated with the coral reef, in shallow water; collected at temperature 29.5°C.

*Excorallana delaneyi* Stone and Heard, 1989

Fig. 3 a-c

**Material examined.** Terminos Lagoon, Gulf of Mexico; EM-9248-f m L:8.3, W:3.2; ov L:9.8, W:2.9; EM-9519 f L:3.6, W:1.2; EM-9224 m L:8.4, W:3.5; ov L:9.1, W:3.5; ov L:9.6, W:3.6; EM-10561 m L:7.0, W:2.6; m L:7.7, W:7.7; m L:8.1, W:2.7; f L:7, W:2.1; f L:5.4, W:1.7; f L:4.6, W:1.5; f L:5.2, W:1.5; ov L:6.7, W:2.0; ov L:7.0, W:2.3; ov L:7.2, W:2.2; ov L:6.2, W:2.1; ov L:7.9, W:2.3; ov L:7.1, W:2.2; ov 9.1, W:3.3; ov L:6.0, W:2.1. Yucalpetén; EM-7530 m L:6.6, W:2.5; EM-7411 m L:8.2, W:2.9; ov L:8.1, W:3.0; ov L:8.4, W:3.2. Río Lagartos; EM-4960 m L:8.8, W:3.0.

**Diagnosis.** Eyes separated. Three cephalic horns in male and two rudimentary horns or tubercles in female;

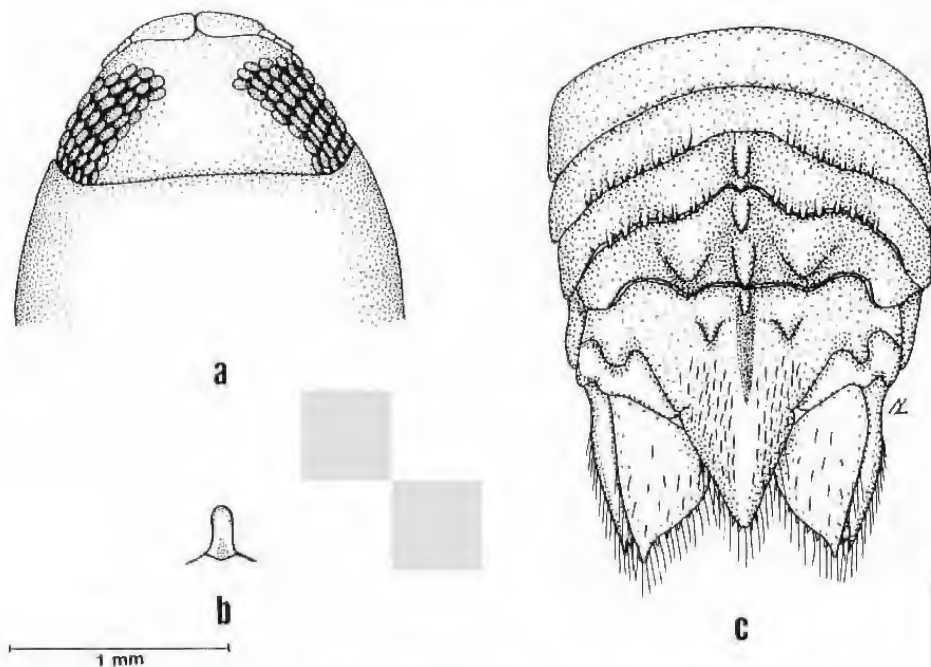


Figure 2. *Excorallana acuticausa* (Miers 1881): a, cephalon; b, frontal lamina; c, telson.

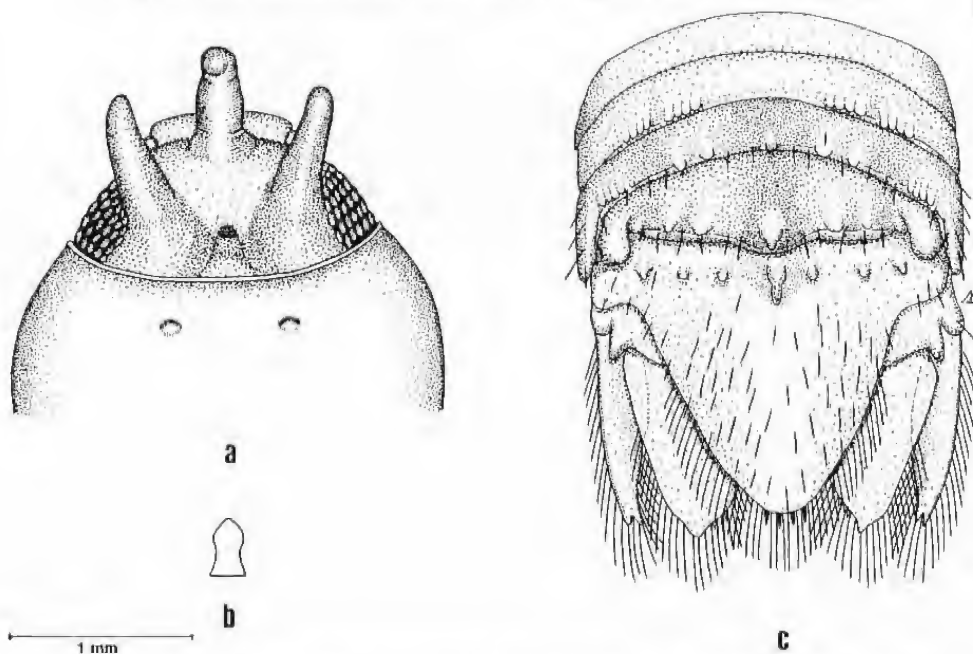


Figure 3. *Excorallana delaneyi* Stone and Heard, 1989: a, male cephalon; b, frontal lamina; c, telson.

rostral horn in male cylindrical similar to the lateral horns. Telson without lateral notches, with four terminal spines, apex weakly crenulate. Frontal lamina elongate, distal end triangular.

**Distribution.** Gulf of Mexico; St. Joseph's Bay, Florida (Stone and Heard 1991). New records: Terminos Lagoon, Campeche; Yucalpetén and Río Lagartos in Yucatan Peninsula.

**Ecological Notes.** Associated with sponges inhabiting *Thalassia testudinum* seagrass beds in shallow water from 0.2 to 2m depth. Also found on sandy bottoms of marsh flats (this study and Stone and Heard 1989).

*Excorallana oculata* (Hansen 1890)

Fig. 4 a-c

**Material examined.** Sacrificios Island off Veracruz, Gulf of Mexico: EM-8768 m L:6.6, W:2.1.

**Diagnosis.** Eyes large, contiguous. Males and females without cephalic horns. Telson with lateral notches. Frontal lamina elongate, narrow, distal tip rounded.

**Distribution.** Caribbean, Brazil, and Annabon Island, Gulf of Guinea, West Africa (Delancy 1989). New record: Sacrificios Island off Veracruz, Southwestern Gulf of Mexico.

**Ecological Notes.** Shallow water, associated with coral reefs.

*Excorallana sexticornis* (Richardson 1901)

Fig. 5 a-d

**Material examined.** Puerto Morelos, Quintana Roo: EM-8556 ov L:6.2, W:2.2; EM-9161-a ov L:7.0, W:2.4; EM-9177-a f L:7.0, W:2.5; m L:6.5, W: 2.0, m L:7.1, W:2.4; m L:6.0, W:2.2; m L:7.5, W:2.3; m L:7.0, W:2.1; EM-9648 m L: 6.4, W:2.1; EM-9687-a m L:7.0, W:2.3; m L:6.0, W:2.1; f L:6.3, W:2.2; f L:7.8, W:2.6; f L:6.0, W:2.1; f L:6.9, W:2.3; f L:7.5, W:2.5.

**Diagnosis.** Eyes normal, separated. Male with four cephalic horns and two on basal segments of first antennae, females with four small tubercles on posterior half of the head. Telson with lateral notches. Frontal lamina short, rounded.

**Distribution.** Key West, Florida (Richardson 1905), Eastern Florida Bay (Rouse 1969), Caribbean (Delancy 1989), Belize (Kensley and Schotte 1989). New record: Puerto Morelos, Quintana Roo, Mexico.

**Ecological Notes.** In shallow water to 1.5m depth in submerged wood and in broken coral heads, at temperatures of 31.5°C.

**Remarks.** The presence of two cephalic tubercles in females of this species was cited by Richardson (1905). Seven of our eight females have four slightly developed cephalic tubercles between the eyes, two located on the same

position as the male's largest horns, and two anterior to these.

*Excorallana subtilis* (Hansen 1890)

Figs. 6 a-g, 7 a-c

**Material examined:** Seibaplaya, Campeche, Southwestern Gulf of Mexico: EM-5610 f L:9.0, W:2.6; Puerto Morelos, Quintana Roo: EM-5705 f L:7.5, W:2.1; EM-9161 f L:6.0, W:2.0; EM-9177 f L:6.9, W:2.3; f L:7.5, W:2.3; EM-9687 ov L:6.0, W:1.8.

**Diagnosis.** Eyes medium in size, separated. Females without cephalic horns or tubercles. Telson with lateral notches. Frontal lamina subquadrate, excavated ventrally.

**Description.** Female; without cephalic horns or tubercles; anterior cephalic margin produced between bases of antennae (Fig. 6a). Eyes medium in size, separated anteriorly by a distance slightly greater than the length of an eye. First antennae with three peduncular articles, basis strongly dilated; with six to eight flagellar articles (Fig. 6b) reaching pereonite I. Second antennae reaching pereonite IV, with 18-21 flagellar articles (Fig. 6c), articles two to eight densely setose. Frontal lamina subquadrate, a little longer than wide, somewhat narrower towards the widely rounded apex and excavated ventrally near the base (Fig. 6d); clypeus narrow, partially concealed; labrum concealed. Maxilliped with epipodite reduced, palp with five segments, with smooth margins, ante-penultimate segment short, penultimate segment curved proximally, tip of distal segment with tuft of setae (Fig. 6e). Right mandible with four subapical cusps, one just below the incisor process, the other three forming the apical part of a medium broad flat tubercle (Fig. 6f); left mandible with three subapical cusps, first and second located below incisor process, third tubercle flat in shape (Fig. 6g); mandibles with lacinia mobilis, without molar process. Pereonites I-VII without dorsal tubercles or setae. Pereopods I-III prehensile; differing among them, in common merus with four short spines on posterior medial margin, ischium with one short spine on posterodistal median margin (Fig. 7a). Pleonites one to five without dorsal tubercles, naked. Pleopods 1-5 with plumose marginal setae. Pleotelson subtriangular, without dorsal setae; two prominent submedian tubercles on dorsal surface near base; margin fringed with setae, lateral margins with deep notches (Fig. 7b); apex rather acute, with two small spines, each tipped with a hair (Fig. 7c). Uropods slightly longer than pleotelson; fringed with setae; uropodal endopod broad, posteriorly subtruncate, distal lateral angles pointed, lateral inner margin armed with six short spines, lateral outer margin with one spine; uropodal exopod less than half the width of the endopod, narrowing to a bifid tip, lateral inner margin without spines, lateral outer margin with one spine.

**Male;** unknown.

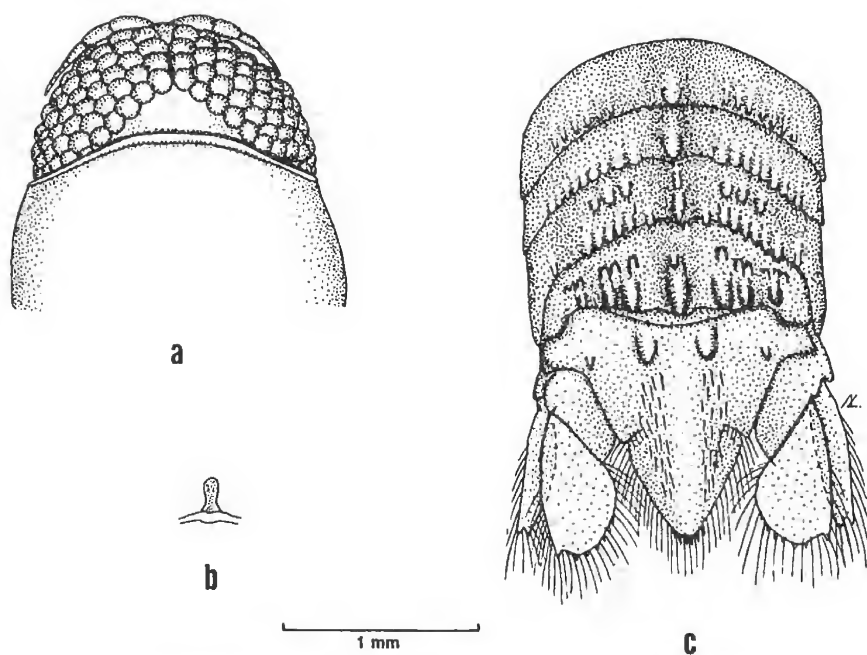


Figure 4. *Excorallana oculata* (Hansen 1890): a, cephalon; b, frontal lamina; c, telson.

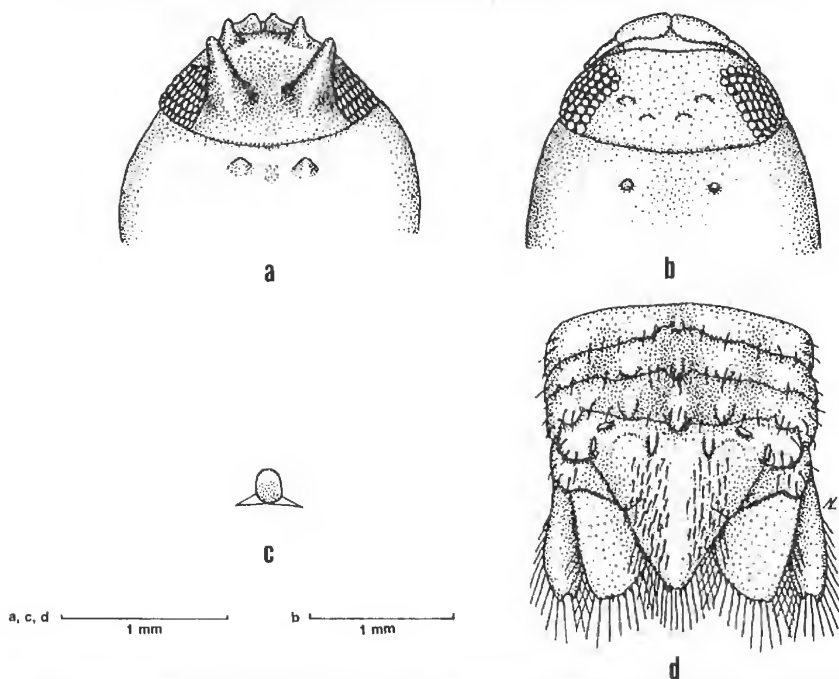


Figure 5. *Excorallana sexticornis* (Richardson 1901): a, male cephalon; b, female cephalon; c, frontal lamina; d, telson.

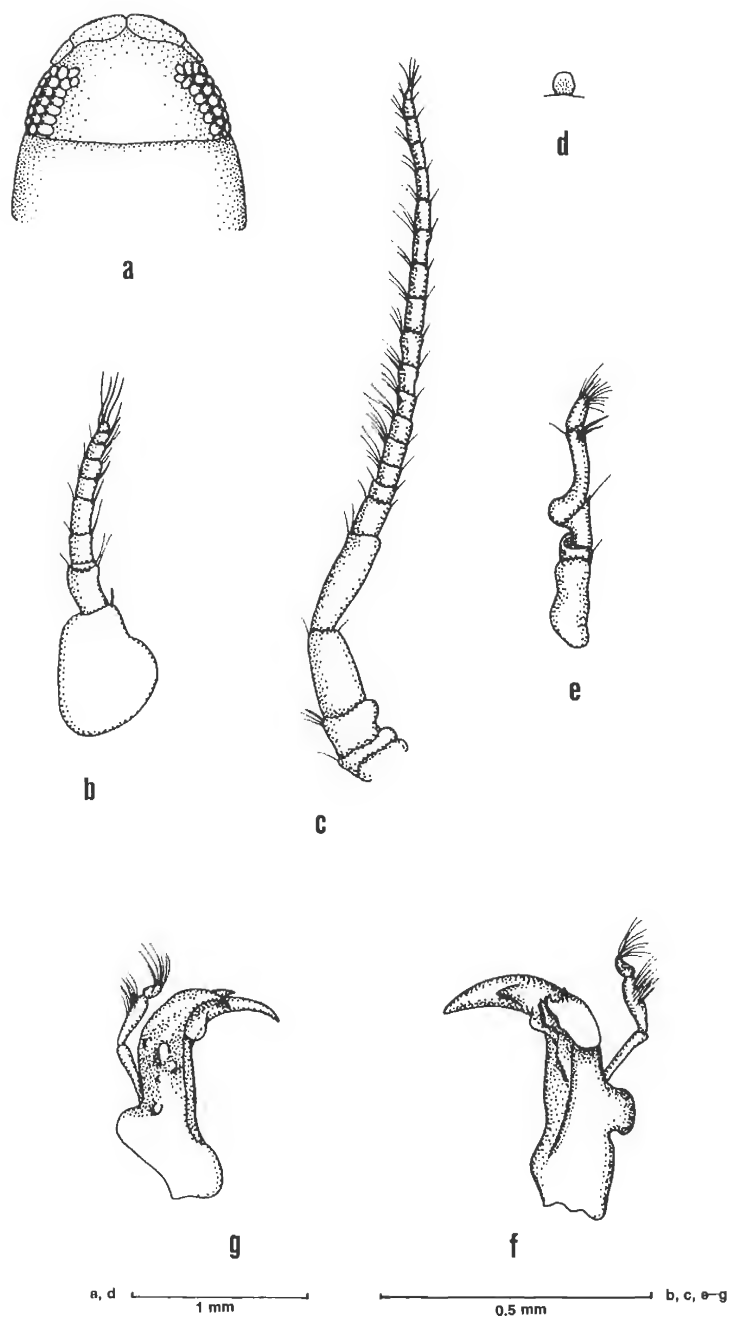


Figure 6. *Excorallana subtilis* (Hansen 1890): a, cephalon; b, first antennae; c, second antennae; d, frontal lamina; e, maxilliped; f, right mandible; g, left mandible.

**Distribution.** St. Thomas, West Indies (Hansen 1890). New records: Seibaplaya, Campeche, southwestern Gulf of Mexico, and Puerto Morelos, Quintana Roo.

**Ecological Notes.** Inhabiting shallow waters from 1 to 2m depth; associated with dead coral heads, algae on coral rock and submerged wood.

**Remarks.** Since Hansen's description (1890) of a single molting female specimen from St. Thomas, the identity of this species has been regarded as uncertain by several authors. Two females of *E. subtilis* were reported by Lemos de Castro and Lima (1971) in Brazil and regarded as a synonym of *E. antillensis* due to their close morphological resemblance and sympatric distribution. The affinity with *E. richardsonae* was also observed in the similarity of the first antennae and frontal lamina. Delaney (1989) mentioned the similarity of *E. subtilis* with *E. acuticauda* and *E. richardsonae*, and considered at the same time *E. antillensis* to be a junior synonym of *E.*

*acuticauda*. Kensley and Schotte (1989) expressed their uncertainty to the identity of the only known specimen. Nevertheless, the redescription of *E. subtilis* from specimens found in the southwestern Gulf of Mexico and the Mexican Caribbean validates the existence of Hansen's species. A comparison with the description of the Brazilian specimens of Lemos de Castro and Lima (1971) shows that the latter specimens belong to a different species due to the presence of tubercles on pleonite 5; the presence of submedial rows of setae along the telson; the lack of the two apical spines; the anterior part of the frontal lamina with a more pronounced angle; the maxilliped with a surface covered with tubercles; and the absence of subapical cusps and lacinia mobilis in both mandibles. Therefore, we consider a species complex formed by *E. acuticauda*, *E. richardsonae*, and *E. subtilis* in which each of the species can be recognized.

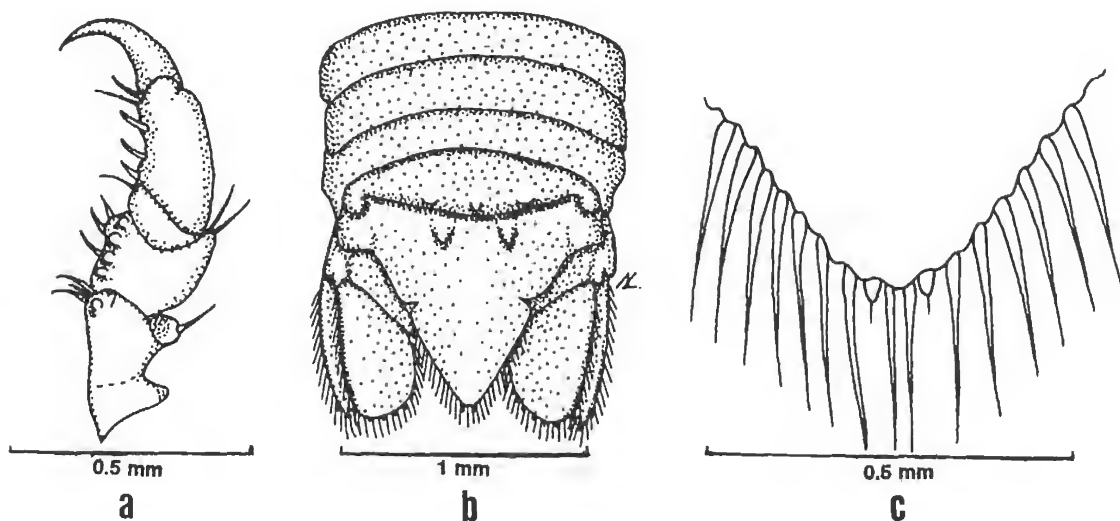


Figure 7. *Excorallana subtilis* (Hansen 1890): a, pereopod I; b, telson; c, tip of telson.

*Excorallana tricornis tricornis* (Hansen 1890)

Fig. 8 a-c

**Material examined.** Terminos Lagoon, Southwestern Gulf of Mexico: EM-9315 f L:4.0, W:1.5; ov L:6.7, W:

1.9; Puerto Morelos, Quintana Roo; EM-5643 m L:6.6, W:2.4; Isla Mujeres, Quintana Roo; EM-7320 m L:6.6, W:2.4; m L:6.0, W:2.3; EM-7327 m L:10.2, W:3.5, m L:10.8, W:3.8, ov L:10.8, W:3.6; EM-7379 m L:7.9, W:3.1; m L:7.8, W:2.9; f L:6.1, W:2.3; ov L:11.0, W:3.7; EM-

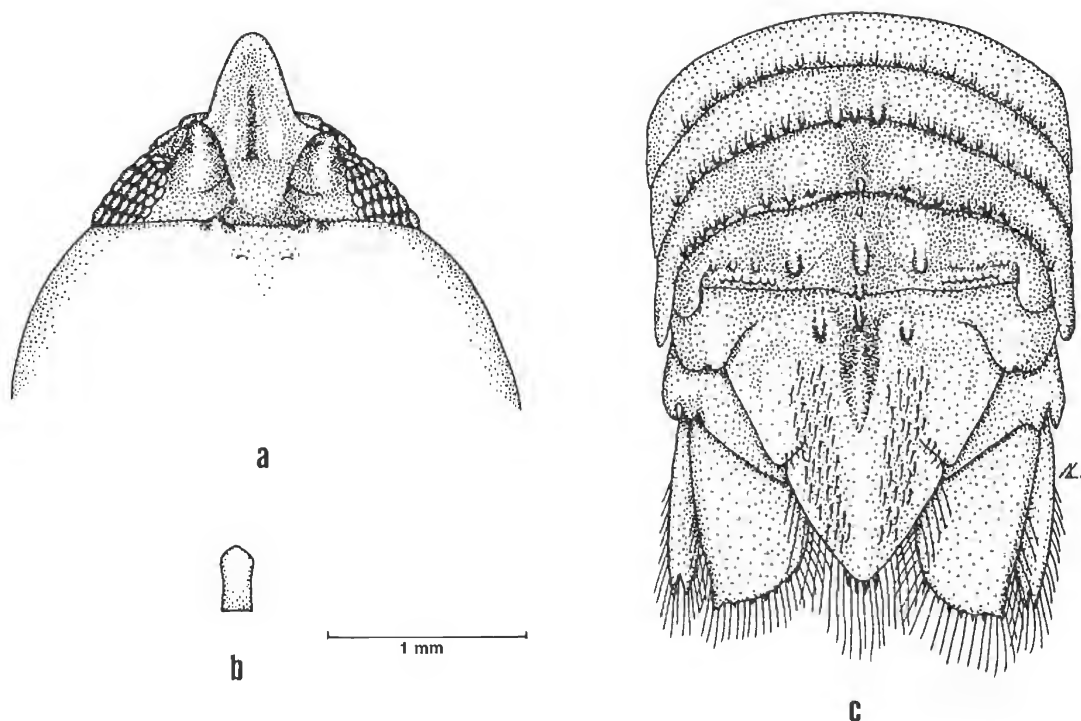


Figure 8. *Excorallana tricornis tricornis* (Hansen 1890): a, male cephalon; b, frontal lamina; c, telson.

7459 ov L:8.5, W:3.0; ov L:7.6, W:2.4.

**Diagnosis.** Eyes separated; male with three cephalic horns, rostral horn concave, broad, lateral horns cylindrical; horns in female rudimentary; telson with lateral notches, apex with four short spines, rows of setae on either side of medial longitudinal area. Frontal lamina elongate, distal end triangular.

**Distribution.** Gulf of Mexico and Caribbean (Delaney 1989). New records: Terminos Lagoon, southwestern Gulf of Mexico; Isla Mujeres, and Puerto Morelos, Quintana Roo, Mexico.

**Ecological Notes.** Reported depths varying from the intertidal to 183m (Delaney 1984) from 44 to 503m (Schultz 1969), and from 18 to 73m in the northeastern Gulf (Menzies and Kruczynski 1983). Found in shallow waters of 1

to 2 m depth in these samples. Material from the Caribbean was found on dead coral heads and submerged rocks. The species was associated with *Thalassia testudinum* seagrass beds in Terminos Lagoon.

*Excorallana warmingii* (Hansen 1890)

Fig. 9 a-c

**Material examined.** No material available in collections in Mexico.

**Diagnosis.** Eyes large, semispherical, contiguous, most of surface of head; males and females without cephalic horns; telson without notches on lateral margins, dorsal surface smooth. Frontal lamina elongate, distal end narrowing and ending in a sphere.

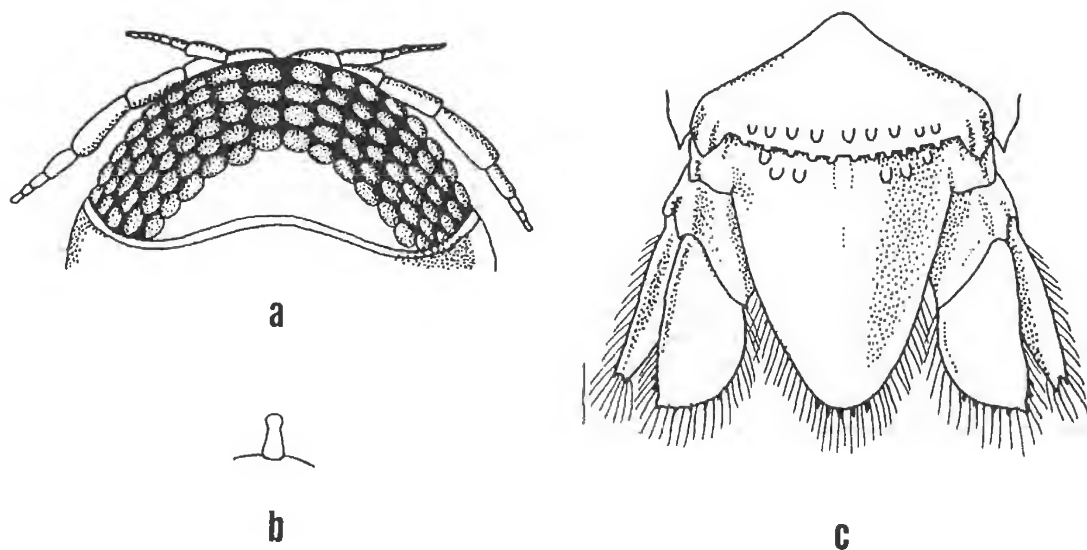


Figure 9. *Excorallana warmingii* (Hansen 1890): a, cephalon; b, frontal lamina; c, telson (after Richardson 1905).

**Distribution.** Off Cape Catoche, Yucatan (Richardson 1905), Caribbean (Delaney 1989).

*Excorallana* sp.  
Fig. 10 a-c

**Material examined.** EM-7601 ov L:9.4, W:2.8.

**Diagnosis.** Eyes large, not contiguous, separated by less than 0.25 the length of an eye; female without cephalic horns or tubercles; telson with lateral notches, dorsal surface smooth. Frontal lamina elongate, narrowing distally, ending in a triangular tip.

**Occurrence.** Puerto Morelos, Quintana Roo.

**Ecological Notes.** Occurs in shallow water at 1.5m depth, associated with coral.

**Remarks.** The ovigerous female of *Excorallana* sp., occurring in Puerto Morelos is an isolated record requiring more material to be described as a new species. Affinities

to the existing species of *Excorallana* are its resemblance to *E. acuticauda* in the lack of cephalic tubercles, the presence of large eyes separated by less than half an eye-length, and the presence of lateral notches on the telson. The female differs from *E. acuticauda* in the smooth dorsal surface of the pleonites, the absence of the median longitudinal depression and the two proximal tubercles on the telson, the shape of the frontal lamina, and the larger eyes. The texture of the dorsal surface of the pleonites has been considered important and has previously been recognized in subspecies differentiation even to its high degree of variability (Bowman 1977; Menzies and Kruczynski 1983). Comparing the female *Excorallana* sp. with females of *E. acuticauda*, the authors discard the possibility that the characters of the former could belong to a juvenile form due to the size and ovigerous state of the specimen, suggesting that it could be a new species.

The following identification key is provided for the seven *Excorallana* species recorded from eastern Mexican waters.

1. Eyes contiguous ..... 2  
    Eyes separated, large or medium in size ..... 3
2. Telson with lateral notches ..... *E. oculata*  
    Telson without lateral notches ..... *E. warmingii*
3. Eyes large; distance between them half or less the length of an eye ..... 4  
    Eyes medium sized; distance between them greater than the length of an eye ..... 5
4. Pleotelson with two submedian tubercles proximally; distance between eyes almost half the length of an eye ..... *E. acuticauda*
5. Telson without lateral notches; adult male with 3 cephalic horns, rostral horn cylindrical; adult female with cephalic tubercles in same position as male horns ..... *E. delaneyi*  
    Telson with lateral notches ..... 6
6. With cephalic horns (males) or tubercles (females) ..... 7  
    Without cephalic horns or tubercles; only females known ..... *E. subtilis*
7. Male with 3 cephalic horns, rostral horn wide at base and concave; female with slightly developed cephalic tubercles in same position as horns in male ..... *E. tricornis tricornis*  
    Male with four cephalic horns, larger ones between eyes, two smaller ones in anterior position, small horns on base of antennular peduncle; female with four small tubercles slightly developed between eyes ..... *E. sexticornis*

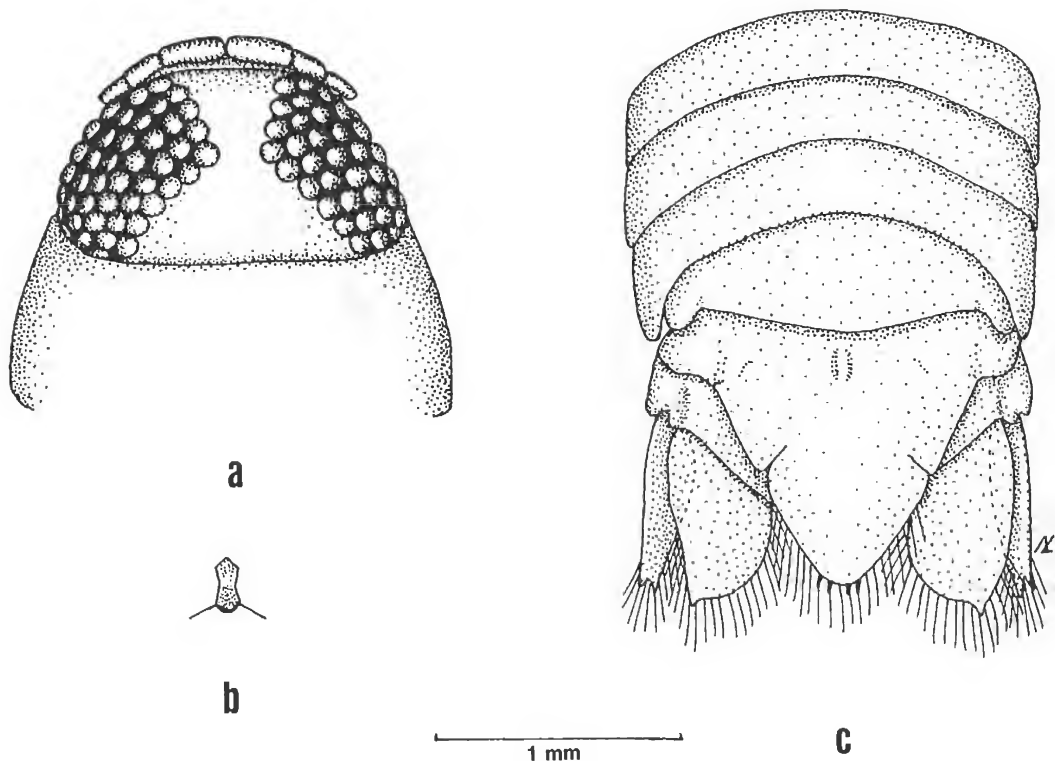


Figure 10. *Excorallana* sp.: a, cephalon; b, frontal lamina; c, telson

## DISCUSSION

Twenty-two species of the genus *Excorallana* have been described for the tropical western Atlantic and eastern Pacific, of which only 20 were included in the revision of the family Corallanidae by Delaney (1989). *Excorallana bicornis* (Lemos de Castro and Lima 1971) was omitted in that list and is herein included as an additional species occurring in the western Atlantic. Occurrence of the genus in the Gulf of Mexico, following Antoine's (1972) subdivision of the Gulf, has been recorded for *E. acuticauda* (Clark and Robertson 1982; Menzies and Kruczynski 1983), *E. delaneyi* (Stone and Heard 1989), *E. mexicana*, *E. tricornis tricornis* (Menzies and Kruczynski 1983), *E. warmingii* (Richardson 1905) and *E. sexticornis* (Rouse 1969). The new records herein extend the range of *E. delaneyi* south in the Gulf of Mexico and increase the number of species occurring in this region to eight with the new reports of *E. oculata* and *E. subtilis* in the Gulf.

Distribution of these species is probably habitat-selective, since most occur in reef patches in the Gulf as well as in seagrass beds. The inclusion of some of the species in the southwestern Gulf of Mexico can be explained by the parasitic behavior reported for *E. tricornis tricornis* (Delaney 1984) and *E. berbicensis* (Stone and Heard 1989) and may follow the distribution patterns of host fish.

Western Atlantic species fall into two groups: a southern group of seven species restricted to the Brazilian coast and part of the Caribbean, and a northern group of 10 species distributed in the Gulf of Mexico, the West Indies and the Caribbean. The geographical distribution of these groups shows a diffused pattern probably related to direct development, besides the geographical barriers.

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# Gulf Research Reports

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## Ecological History, Catastrophism, and Human Impact on the Mississippi/Alabama Continental Shelf and Associated Waters: A Review

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## ECOLOGICAL HISTORY, CATASTROPHISM, AND HUMAN IMPACT ON THE MISSISSIPPI/ALABAMA CONTINENTAL SHELF AND ASSOCIATED WATERS: A REVIEW

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**ABSTRACT** The Mississippi/Alabama continental shelf and associated coastal waters together form a complex ecological system of interrelated parts. The biological system of the area has become established during the period of sea level rise following the last continental glacial maximum about 18,000 years ago. Contemporary biological populations of the inshore waters are subject to episodic catastrophic events caused by exceptional cold fronts, flooding, major storms, hypoxia, red tide outbreaks, and major droughts. Most of these events are not known to affect the shelf populations directly, but indirect effects through food chain disruptions are likely. Loop Current intrusions and entrainment of deep Gulf waters could directly impact the shelf species. Imposed upon these events are various human intrusions which have severely reduced the quality and quantity of inshore habitats. Increase in commercial and recreational fishing pressure in the inside waters and on the continental shelf during the past two decades has been accompanied by dramatic decline in populations of demersal and pelagic fish species. In order to be able to manage resources of the area successfully, there is an urgent need to understand the natural functioning of the entire complex ecological system.

### INTRODUCTION

The Mississippi/Alabama continental shelf and the surrounding marshes, bays, estuaries, and lagoons form a large complex ecological system of interconnected components. The subsystems are related through the flow of nutrients, suspended particulates, and migratory species. Major efforts to bring portions of this system into focus include those of Christmas (1973), Darnell and Kleypas (1987), and Vittor (1985). However, virtually all of our knowledge of the larger system derives from study of individual components, and dynamic relations between the subsystems are poorly understood. Yet a comprehensive understanding of the larger system is essential if management efforts are to be successful in maintaining basic ecological relationships in the face of mounting human intrusion. The present article provides a focus on the larger system by reviewing pertinent literature concerning ecological history, natural catastrophic events, and human impacts. This is viewed as a necessary first step in examining the larger picture.

### ECOLOGICAL HISTORY

During Pleistocene time, the coastal and continental shelf environments off Mississippi and Alabama underwent dramatic changes. Associated with repeated advance and retreat of the continental ice sheets, the sea level receded nearly to the outer edge of the continental shelf and then rose again to approximately its present stand or higher. With each retreat of the sea, the shelf became exposed to subaerial erosion and oxidation, and streams passing through

the area carved deep valleys. Subsequent rise in sea level saw filling of the valleys and smoothing of the surface. Associated changes involved shifting of the position of the Mississippi River delta, barrier island formation and destruction, and formation and filling of bays and estuaries.

Following the last glacial maximum about 18,000 years ago, the sea level has risen to its present stand, and repopulation of the northern Gulf shelf, bays, and estuaries has taken place. New tropical immigrants brought in by the Gulf Loop Current and possible other means (Humm and Darnell 1959; Darnell and Kleypas 1987) have been added to the normal biota of the northern Gulf. Considering the variability of the environments, the recency of their availability, and the periodic addition of new faunal elements from the south, it is reasonable to conclude that the processes of genetic adjustment are still underway.

This conclusion is borne out by the fact that at least the key species of the ecological system appear to exhibit R-type life history strategies—that is, they are opportunistic pioneering species with short life histories and high reproductive rates. They are adapted for rapid exploitation of new ecological opportunities and for persistence in the area despite local habitat loss, great variability in environmental factors, and the occasional occurrence of natural catastrophes. These key species include the brown and white shrimp, blue crab, gulf menhaden, sand seatrout, spot, Atlantic croaker, and striped mullet (all estuary dependent), as well as the longspine porgy and several flatfish (non-estuary dependent). Despite wide annual variations in abundance, these species have persisted and flourished in the area and have contributed to the stability of the shelf ecological system.

## NATURAL CATASTROPHISM

The coastal environments of the northern Gulf of Mexico undergo regular cycles of seasonal changes in atmospheric, hydrographic, and oceanographic factors. Likewise, the life histories of the various species involve annual responses to the regular environmental changes (Benson 1982). However, on the continental shelf and in

related coastal environments of the Mississippi-Alabama area, certain major changes occur irregularly, and these episodic events may interrupt the normal biological patterns. Some are known to result in mass mortalities, and probably place major stress on populations of the area. Biological effects of these events (Table 1) have not been studied adequately.

TABLE 1

Major catastrophic events which affect the environments and biota of the Mississippi-Alabama marine systems.

| Catastrophic Events         | Effects   |  |
|-----------------------------|---|--|
|                             | Estuaries   | Continental Shelf  |
| Cold fronts                 | Recorded from Mississippi and Alabama<br><br>Can cause mass mortality of invertebrates and fishes.  | Not known to affect species on the shelf but may induce some stress.<br><br>Probably limits establishment of tropical species in shallow water habitats.   |
| Floods                      | Recorded around Mississippi River Delta, Lake Pontchartrain, Lake Borgne, Mississippi Sound, and Mobile Bay.<br><br>Short term effect is to place much fresh water, sediment, and debris into estuaries, destroy bottom habitat and oyster reefs, and kill or chase out mobile species.<br><br>Long term effect is to bury pollutants and increase fertility. | Recorded from the southwestern half of the shelf.<br><br>Short term effect is to increase young fishes on the inner shelf and move older fishes to deeper water.<br><br>Long term effect may be to increase fertility. |
| Major storms and hurricanes | Affect entire coastline<br><br>Cause major flooding and extensive habitat damage (sedimentation of bottoms, destruction of marshlands and submerged vegetation, burial of oyster reefs, and erosion of shorelands).   | Affect the entire coastline.<br><br>Induce strong currents; stir up bottom sediments to a depth of 8 m or more; may restructure barrier islands.<br><br>Biological effects unknown.                                    |
| Hypoxic events              | Known from Lake Pontchartrain and Mobile Bay.<br><br>May cause mass mortality of invertebrates and fishes.  | Not known from the Mississippi/Alabama continental shelf.  |
| Red tide outbreaks          | Recorded from Chandeleur Sound, Lake Borgne, Mississippi Sound, and Mobile Bay.<br><br>Small fish kill reported.  | Reported between and near barrier islands off Louisiana and Mississippi.   |

### Cold fronts

During exceptional winters, major cold waves strike the northern Gulf Coast and rapidly chill the estuarine and lagoonal waters. Immobilized by the sudden chill, invertebrates and fishes are unable to escape and die in great numbers. Such events have been reported along most of the northern Gulf Coast from south Texas through the Florida peninsula. Low temperature fish kills have been reported from coastal waters of Mississippi (Christmas 1973; Overstreet 1974) and from Mobile Bay (Reagan 1985; Johnson and Seaman 1986). No effects of low temperature have been reported for populations of the shelf, but it is likely that some tropical species which have become established on the shelves of south Texas and peninsular Florida are excluded from the Mississippi-Alabama shelf by exceptional extremely cold conditions.

### Floods

Flooding of low coastal areas in the Mississippi River delta was a normal occurrence prior to the construction of artificial levees (Gunter 1952). Today it occurs east of the delta when the Bonnet Carré spillway is opened to permit floodwaters to pass through Lakes Pontchartrain and Borgne and Mississippi Sound to the Mississippi-Alabama shelf. Flooding may also occur when heavy rains fall in the drainage basins of the coastal streams, particularly the Pascagoula and Mobile Rivers, or when the coastal areas themselves are inundated from winter rainstorms or summer tropical depressions. The immediate physical effects are to replace or greatly dilute the saline waters of bays, estuaries, and sounds; markedly increase the level of suspended sediments; reduce oxygen values in the hypolimnion; and deposit a carpet of new sediments on the bottom (Schroeder 1977; Schroeder *et al.* 1990). Runoff erodes the banks and may bring much terrestrial debris into the bays and estuaries. Depending upon the season, the freshwater inflow may cause a dramatic temperature shift. These physical changes may also occur on the continental shelf if the flooding is persistent.

Biological effects of flooding in the Mississippi-Alabama area have been reported by Butler (1952), Butler and Engle (1950), Christmas (1973), Dardeau *et al.* (1990), Dawson (1965), Gunter (1952, 1953, 1979), Hawes and Perry (1978), Poirrier and Mulino (1975, 1977), Russell (1977), and Stout (1990). Marine plankton is replaced by freshwater species within bays and sounds (Hawes and Perry 1978; Simmons and Thomas 1962; Thomas and Simmons 1960). Some benthic species die, and bottom areas suffer a reduction in species abundance and diversity. Immobile forms such as the American oyster are buried, and large populations simply perish (Butler 1952; Butler and Engle 1950; Stout 1990). The young of estuary-related

species, such as shrimp and the Atlantic croaker, are unable to penetrate to the estuaries and remain on the inner continental shelf. Adults are forced to move to deeper waters of the middle or outer shelf (Russell 1977). Mortality among these mobile species is not known, but certainly there must be major losses among the eggs, larvae, and juveniles which are barred from entering the nursery areas. The blanket of sediments deposited is generally rich in nutrients so that when recovery begins the following year, biological production may be higher than normal for a few years thereafter.

### Major storms

Major storms and hurricanes frequently strike the northern Gulf Coast, accompanied by high winds, torrential rains, elevated sea levels, heavy wave action, and extensive coastal flooding. Strong water currents are generated out on the continental shelves, and bottoms may be stirred to a depth of at least 80 m/260 ft (Dinnel 1988). Impacts on coastal waters and on barrier islands and other land forms may be dramatic. Effects of major storms on the biota of bays and estuaries of the area have received little attention, but they have been addressed by Dardeau *et al.* (1990) and Stout (1990). Since the storms are generally accompanied by heavy precipitation, all the effects of flooding discussed above occur. In addition, the waves and strong water currents may cause direct physical damage to hard bottom species such as oysters, uproot submerged vegetation, tear up marshlands, and bury soft bottom species (Stout 1990). There have been no reports on the effects of major storms on the biota of the Mississippi-Alabama continental shelf.

### Hypoxic events

Waters of the bays, lagoons, and continental shelf normally contain high levels of dissolved oxygen. However, the oxygen in the near bottom waters may be reduced to very low levels (hypoxia) or used up completely (anoxia) under conditions of high organic loading, rapid bacterial decomposition, and poor circulation (often due to summer stratification of the water column). Seawater is rich in sulfates, and under anoxic conditions, the sulfate becomes chemically reduced to the highly-toxic hydrogen sulfide gas and metal sulfides, some of which are soluble in seawater. Depending upon the severity of the event, hypoxia may induce avoidance, stress, or death in a few sensitive species, or it may result in mass mortality in many species due to asphyxiation and hydrogen sulfide intoxication.

In the Mississippi-Alabama area, hypoxia has been reported from Lake Pontchartrain (Junot *et al.* 1983; Poirrier 1979; and Sikora and Sikora 1982), St. Louis Bay,

Biloxi Bay, Pascagoula River marshes (Christmas 1973), and Mobile Bay (Dardeau *et al.* 1990; Loesch 1960; May 1973; Schroeder and Wiseman 1988; and Schroeder *et al.* 1990). In Lake Pontchartrain, low diversity in benthic communities accompanied hypoxic conditions. Small fish kills have been associated with hypoxia in Mississippi. In Mobile Bay, severe summer hypoxia results in mass avoidance and mass mortality of many invertebrate and fish species. Hypoxic conditions have not been reported from the Mississippi-Alabama continental shelf area.

### Red tide outbreaks

Phytoplankton blooms are a regular occurrence in the inshore and nearshore waters of the northern Gulf. Two phytoplankton species produce chemical substances into the water which are extremely toxic to other marine life. These are the dinoflagellates *Gonyaulax monilata* and *Ptychodiscus brevis*. When appropriate conditions prevail, extremely dense populations of one of these species may develop, giving the surface waters a reddish tint. Hence, the occurrence is called a "red tide." Such events have been recorded off most of the northern Gulf Coast. In the Mississippi-Alabama area, a single red tide event was reported by Perry *et al.* (1979) due to a bloom of *Gonyaulax monilata*. This bloom persisted for about two weeks until dissipated by a hurricane. It was most intense in the western sector of Mississippi Sound south of St. Louis Bay, in the pass between Cat and Ship Islands, and in the upper portions of Chandeleur Sound. Lower concentrations extended eastward through Mississippi Sound into Alabama and on the nearshore shelf off Horn and Petit Bois Islands. Some of the Alabama blooms were apparently heavy (Perry *et al.* 1979). Only a small fish kill was reported.

### Other events

The present section has documented five types of natural catastrophic events which may affect coastal populations of the Mississippi-Alabama area. Two additional types of events may be added to this list. Prolonged droughts reduce the amount of freshwater entering coastal bays and estuaries, leading to greatly elevated salinity levels in the inside waters. Populations of mobile and immobile estuarine species with low salinity tolerances are greatly reduced and replaced by high salinity forms. Normally excluded marine parasites and predators range freely and exact a significant toll on oysters and other estuarine species (Stout 1990). Another event of possible significance is the periodic intrusion of Loop Current water or of deep Gulf water up DeSoto Canyon. However, nothing is known about the biological consequences of such intrusions.

### Implications of natural catastrophic events

The episodic events reported here often cause mass mortalities which can lead to major fluctuations in population abundances of the coastal species. Although the primary effects are generally felt by species inhabiting the inside waters, some of the events directly affect populations of the continental shelf. In either case, the ecological systems of the shelf are affected through reduction in food supplies and subsequent modification of the shelf food chains. Except for extreme cold weather which may limit the distribution of tropical species, none of the events is likely to eliminate species populations from the area. Although recovery from an event eventually takes place, population levels may be reduced during and after an event, and the surviving individuals probably are under some measure of physiological stress. Thus, they would be more susceptible to additional stress imposed by human activities. Considering the wide fluctuations imposed upon the populations by natural events, discernment of the impacts of specific human activities may be extremely difficult.

### HUMAN INFLUENCES

Estuary-related species of the Mississippi-Alabama area utilize four basic nursery areas and appear to migrate seaward through the passes (Figure 1). Such migratory pathways would be consistent with adult distribution patterns observed on the continental shelf (Darnell 1985). In any event, this division of the nursery areas provides a convenient basis for the discussion of the local human activities and their major environmental effects (Table 2).

#### Area 1 - Mississippi River delta through Biloxi marshes

Human activities and their effects in this area have been addressed by Craig and Day (1977), Craig *et al.* (1979), Gagliano and vanBeek (1970), and Rounsefell (1964). Leveeing of the lower Mississippi River during the past century has deprived much of the lower delta of its normal annual nourishment of silt. As a result, subsidence and erosion are causing a land loss of over 14 feet per year. The Mississippi River Gulf Outlet Canal constructed in the early 1960s and related waterways have modified drainage patterns and permitted saltwater intrusion well into the productive Biloxi marshes.

#### Area 2 - Lake Pontchartrain through western Mississippi Sound

Human activities and environmental effects in this area have been discussed by Craig *et al.* (1979), Christmas

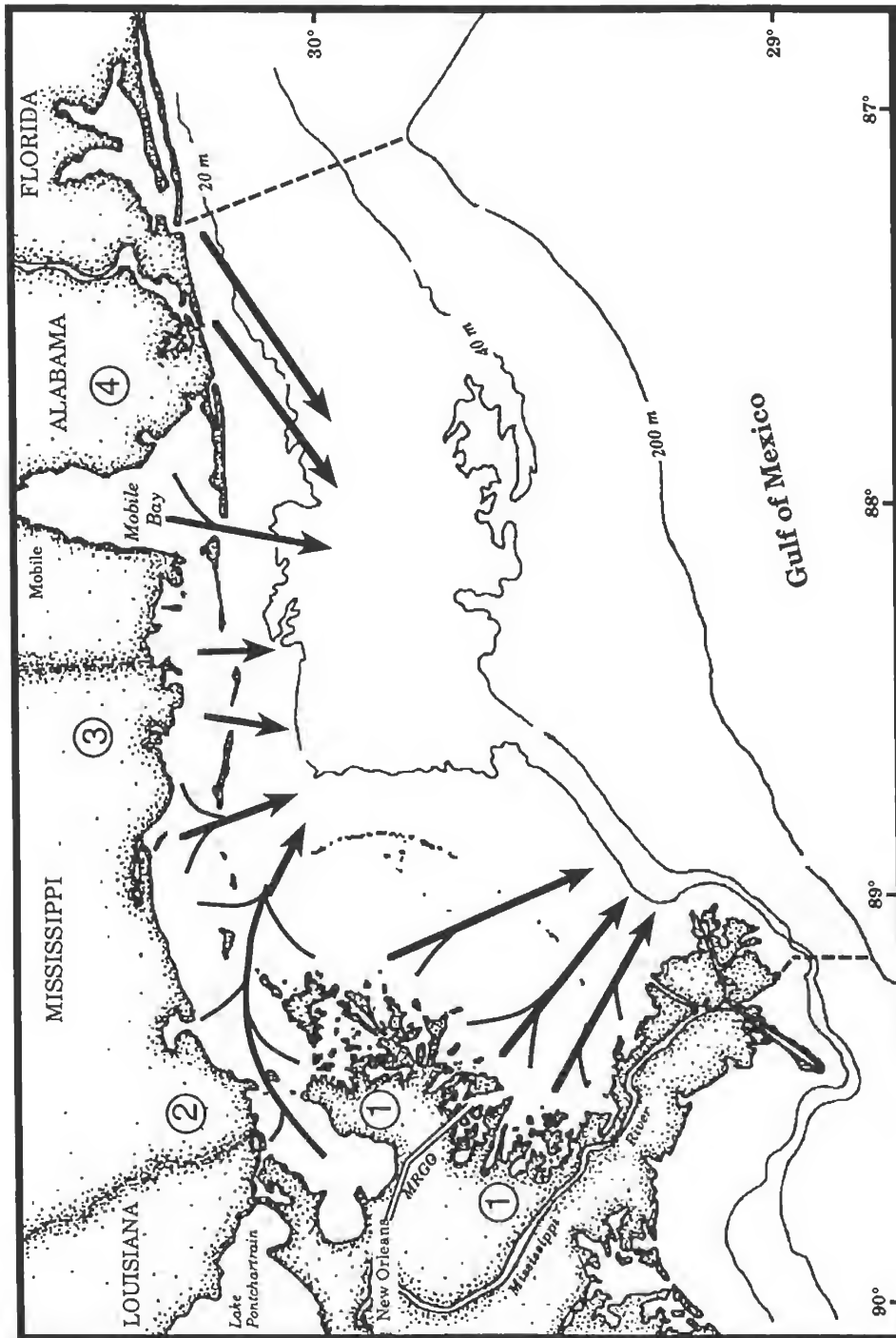


Figure 1. Estuarine nursery areas and presumed migratory pathways for estuary related species which inhabit the Mississippi/Alabama continental shelf.

TABLE 2

Summary of human activities and major effects on estuarine and continental shelf environments of the Mississippi-Alabama area.

| Human Activities  | Major Environmental Effects              |
|---|--|
| <b>Estuarine areas</b>  |  |
| <u>Area 1. Mississippi River Delta through Biloxi Marshes</u>       |  |
| - Leveeing of Mississippi River                                     | - Loss of estuarine habitat              |
| - Channelization of marshes   | - Saltwater encroachment                 |
| <u>Area 2. Lake Pontchartrain through western Mississippi Sound</u> |  |
| - Leveeing and revetment of shorelines                              | - Loss of estuarine habitat              |
| - Land development  | - Reduction of submerged vegetation      |
| - Shell dredging  | - Loss of organic detritus food resource |
| - Dumping of municipal and industrial wastes                        | - Deterioration of soft bottoms          |
| - Agricultural runoff   | - Saltwater intrusion                    |
|   | - Eutrophication                         |
|   | - Creation or intensification of hypoxia |
|   | - Accumulation of chemical pollutants    |
| <u>Area 3. Central and eastern Mississippi Sound</u>                |  |
| - Land development  | - Loss of estuarine habitat              |
| - Dredging and spoil placement                                      | - Interference with natural circulation  |
| - Dumping of municipal and industrial wastes                        | - Creation or intensification of hypoxia |
|   | - Chemical pollution                     |
| <u>Area 4. Mobile Bay through Pensacola Bay</u>                     |  |
| - Land development  | - Loss of estuarine habitat              |
| - Dredging and spoil placement                                      | - Reduction of submerged vegetation      |
| - Channelization  | - Modification of circulation            |
| - Addition of municipal and industrial wastes                       | - Saltwater intrusion                    |
| - Agricultural runoff   | - Creation or intensification of hypoxia |
| - Logging   | - Chemical pollution                     |
| <b>Continental Shelf</b>  |  |
| - Overfishing   | - Drastic reduction in fish populations  |

(1973), Englande *et al.* (1979), Junot *et al.* (1983), Poirrier (1979), Sikora and Sikora (1982), Sikora *et al.* (1981), Stone (1980), Stone *et al.* (1982), and Turner *et al.* (1980). During the past four decades, the environment of Lake Pontchartrain has been modified substantially by human activities (Stone *et al.* 1982). Levees and stone revetments placed along the south shore have cut off shallow wetlands and reduced wave erosion of the marshes. As a result, prime nursery areas have been sealed off, and the major source of organic detritus, formerly important in the local food chains, has been eliminated. Persistent and extensive shell dredging has reduced most of the lake bottom to a thin clay gel incapable of supporting the weight of adult rangia clams (Sikora *et al.* 1981). Virtual elimination of rangia and other benthic species has further reduced the food supply for estuary-related species (Sikora *et al.* 1981). Disposal into the lake of large volumes of domestic sewage by municipalities of Jefferson Parish and street runoff by the city of New Orleans have added organic matter and many chemical pollutants. Additional pollutants now enter the lake from agricultural and industrial sources along the northshore streams and from the industrial canal. The latter permits intrusion of a bottom saltwater wedge bringing various heavy metals and a high oxygen demand. Hypoxic areas or "dead zones" now occur periodically off the mouth of the industrial canal and extend well into the lake (Sikora and Sikora 1982). Frequent openings of the Bonnet Carré spillway during the past two decades have caused long periods of low salinity and high turbidity and have added fine sediments and additional chemical pollutants to the lake. Recent surveys have shown the submerged vegetation beds to be greatly reduced (Turner *et al.* 1980). As a result of these various human intrusions, the usefulness of the lake as a nursery area for estuary-related species has been greatly diminished.

The Pearl River marshes still appear to be largely intact, but sulfites and other chemicals from upstream paper mills and other industry may be reducing water quality. St. Louis Bay is affected by excess BOD loading, and hypoxic conditions with associated fish kills have been reported from this area (Christmas 1973).

#### Area 3 - Central and Eastern Mississippi Sound

Human activities and their effects in this sector have been reported by Christmas (1973) and McBee and Brehm (1979). The increasing human population has given rise to considerable land development, dredging and spoil placement, and dumping of municipal and industrial wastes. Such activities have been particularly prominent around St. Louis Bay, Biloxi Bay, and low reaches of the Pascagoula River. This has resulted in considerable loss of estuarine habitat, chemical pollution, and the creation or intensifica-

tion of local hypoxic events accompanied by fish kills. Channel dredging and spoil placement have modified circulation patterns within the bays and facilitated saltwater intrusion (Christmas 1973). Spoil banks extending across the eastern sector of Mississippi Sound have created a virtual dam, resulting in separate circulation patterns east and west of the banks. Undoubtedly, these spoil banks constitute a barrier to the movement of many marine species as well.

#### Area 4 - Mobile Bay through Pensacola Bay

Human activities and environmental effects in the eastern sector have been discussed by Dardeau *et al.* (1990), Friend *et al.* (1981), Horn (1990), Isphording and Flowers (1990), Schroeder *et al.* (1990), and Stout (1990). Mobile Bay has been modified extensively by land development, dredging and spoil placement, channelization, logging, influx of municipal and industrial wastes, and upstream channelization and agricultural runoff into the Mobile River (Stout 1990). Documented changes in the bay include considerable loss of estuarine habitat and over 35 percent reduction of submerged vegetation beds. Remaining beds are being replaced by introduced and less desirable species (Stout 1990). Circulation patterns have been altered by dredging and creation of spoil mounds, ridges, and islands. Channelization has facilitated saltwater intrusion (Schroeder *et al.* 1990). Chemical pollution of the waters, sediments, and oyster tissue is severe (Isphording and Flowers 1990). Hypoxia in the bay appears to be a natural event, but certainly it has been exacerbated by human activities, especially through restriction of circulation and the addition of oxygen-demanding chemicals (Schroeder *et al.* 1990). Perdido and Pensacola Bays are less severely affected by human activities, but land development has reduced estuarine habitat, and some municipal and industrial pollution has occurred.

As noted by Darrell *et al.* (1976), certain river basin modifications may have profound effects on coastal systems. Upstream damming, channelization, and leveeing of floodplains are particularly important. In general, these entail retention of sediments and reduction in coastal beach nourishment. They often result in abnormal seasonal freshwater flow patterns in the receiving bays and estuaries. They may also diminish the contribution of leaf litter and other organic detritus from floodplains, thereby reducing the base of organic material supporting the coastal ecosystems. Stout (1990) discussed a number of anthropogenic changes in river basins feeding Mobile Bay, but specific biological effects were not documented. The recent opening of the Tennessee-Tombigbee Waterway could greatly influence the ecology of Mobile Bay, but no information has been found on effects of this development.

### Continental shelf

The Mississippi-Alabama continental shelf has been modified by dredging and spoil disposal, channelization, creation of artificial reefs, and limited development of oil and gas resources (Vittor 1985). Whatever the local influences may have been, these activities are not considered to have caused major or widespread effects on the environment or biota. Commercial fishing on the shelf has been growing since the Second World War, and it has been particularly intense during the past 1½ decades (Browder *et al.* 1990). Activities include purse seining for menhaden, trawling for demersal shrimp and fish species, and use of hook-and-line (trolling, bottom fishing, and longlining) for reef-related as well as coastal and offshore pelagic species. The port of Pascagoula, Mississippi reports the second highest level of commercial fish landings in the nation (U.S. Dept. of Commerce 1991). Since 1980, there has been a dramatic increase in the harvest of reef-related and pelagic species (Browder *et al.* 1990). Recreation fishing also has increased greatly during this period, with more fishermen using party/charter boats and private or rented craft capable of harvesting deeper reefs and larger pelagic species. Incidental fish species taken in the menhaden

fishery have been reported by Christmas *et al.* (1960), and those caught by bottom trawls are listed in Darnell (1985), Darnell and Kleypas (1987), Franks *et al.* (1972), and McEachran *et al.* (1992). Invertebrates taken by bottom trawls have been reported by Defenbaugh (1976), Franks *et al.* (1972), and Soto (1972).

Intensified fishing efforts have been accompanied by alarming declines in the estimated sizes of remaining fish stocks (Browder *et al.* 1990; Brown *et al.* 1990). Data for these estimates (Figures 2-5) encompass the shelf area from west of Barataria Bay, Louisiana to DeSoto Canyon, and are pertinent to the Mississippi-Alabama shelf (Browder, personal communication). Between 1960 and 1988, the menhaden harvest more than doubled and the shrimping effort almost quadrupled (Figure 2). Between 1972 and 1987, the biomass of bottom fishes declined from 116 kg/ha to around 26 kg/ha, approximately 22 percent of the original level (Figure 3). Despite greatly intensified fishing effort, the annual red snapper harvest declined between 1979 and 1986 from 16 million to about 4.5 million pounds (Figure 4). During the same period, the spawning stock of king mackerel declined to about one-third of its former level (Figure 5). Similar decreases have been observed for Spanish mackerel as well as in offshore pelagic species

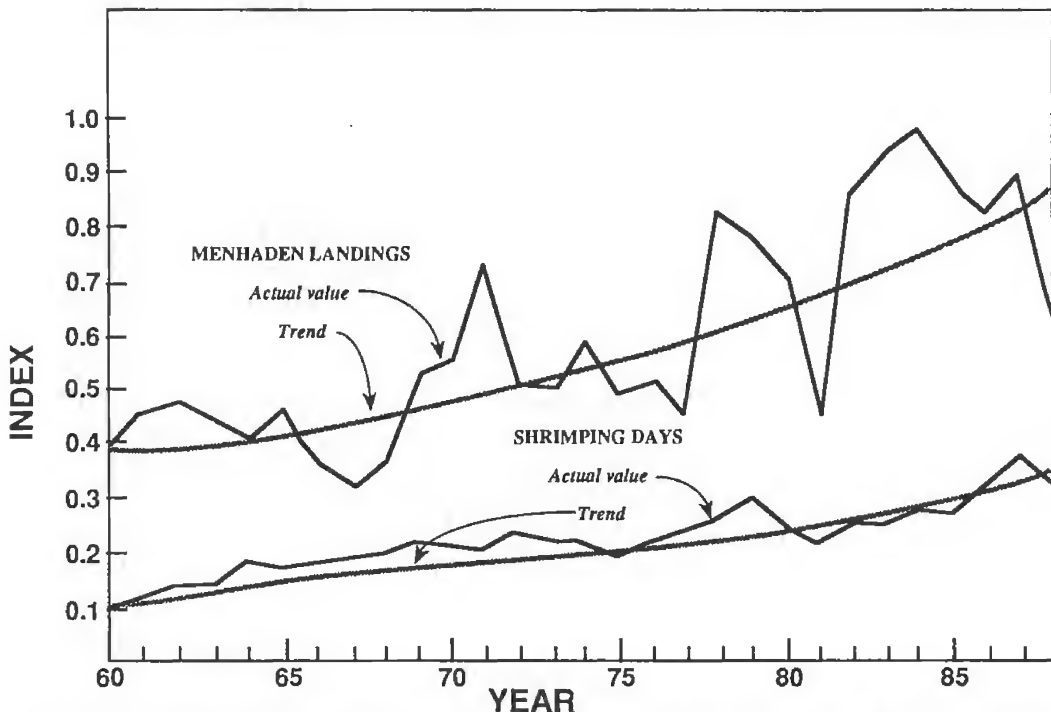


Figure 2. Trends in the harvest of menhaden and shrimping effort on the north central Gulf shelf between 1960 and 1988. (After Browder *et al.*, 1990 and Brown *et al.*, 1990.)

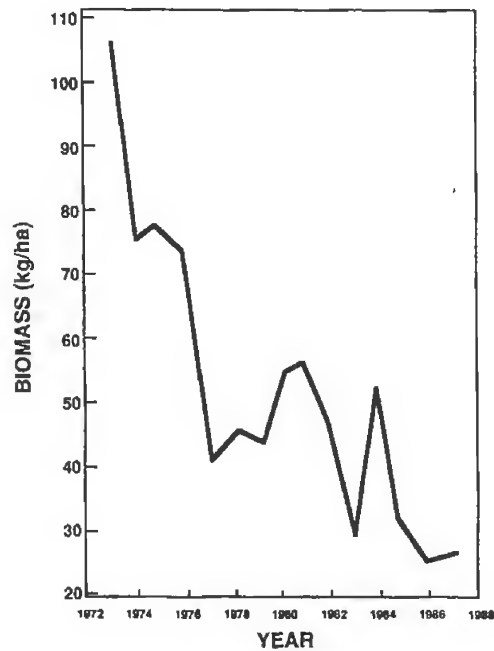


Figure 3. Estimated biomass of bottom fishes on the north central Gulf shelf between 1972 and 1987. (After Browder *et al.* 1990 and Brown *et al.* 1990.)

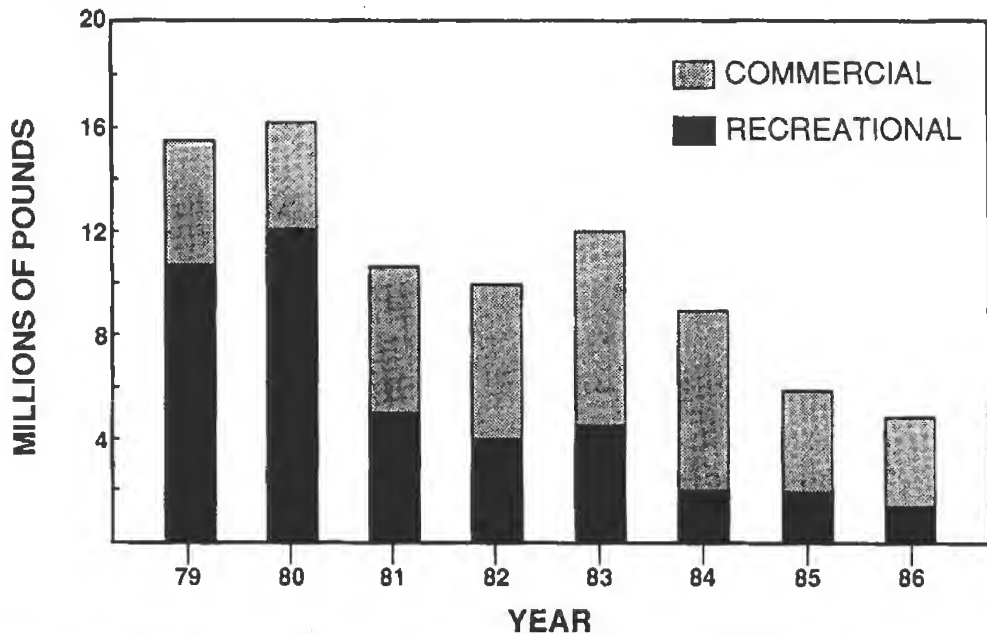


Figure 4. Commercial and recreational harvest of red snapper in the north central Gulf between 1979 and 1986. (After Browder *et al.* 1990 and Brown *et al.* 1990.)

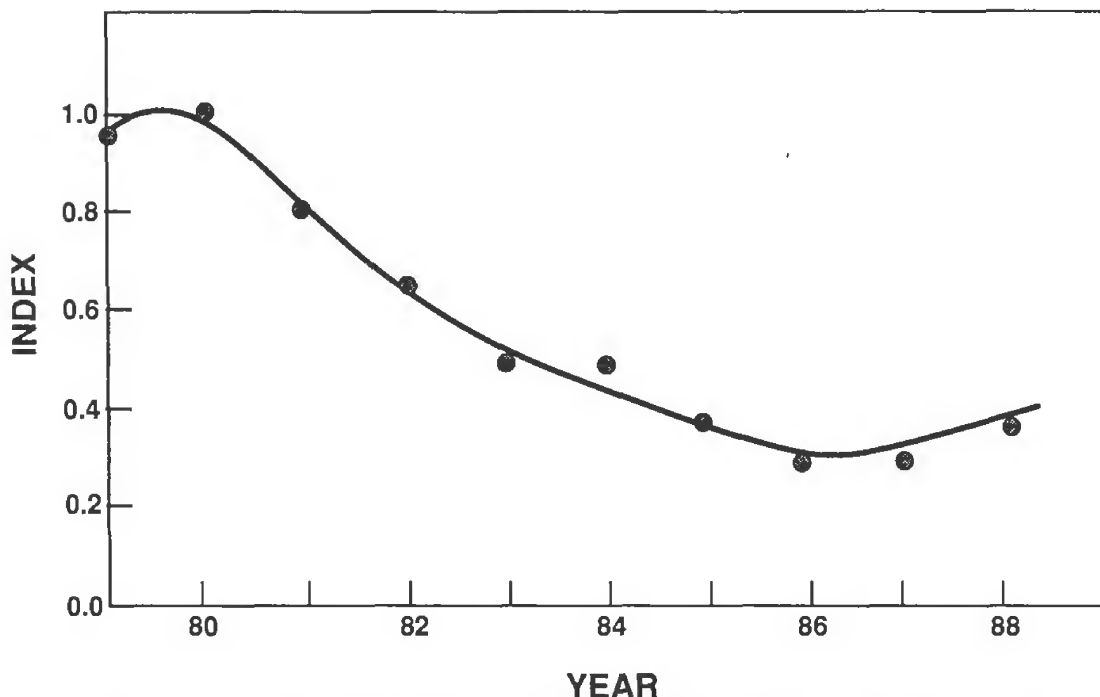


Figure 5. Estimated spawning stock of the king mackerel in the north central Gulf from 1979 through 1988. (After Browder *et al.* 1990 and Brown *et al.* 1990.)

(including bluefin tuna, swordfish, and others). Overfishing appears to be the primary reason for the declines. However, as noted earlier, there has been a simultaneous reduction in both the extent and quality of the nursery areas for estuary-related species. Significant diminution in the annual crop of estuary-related species would reduce the level of prey species and modify food chains of the continental shelf. In turn, this would likely be reflected in food chains supporting the larger predators just beyond the shelf edge. Undoubtedly, both overfishing and inshore habitat deterioration are responsible for this decline of fish stocks.

#### CONCLUSIONS

The Mississippi-Alabama continental shelf and related coastal waters have undergone certain long-term changes related to Pleistocene sea level stands. On shorter time scales, the system is subject to modification by natural catastrophic events, some of which may alter population levels over periods of one or two years. Imposed upon these

natural trends and events is the recent massive intrusion by human activities which has had major effects upon the nearshore and possibly offshore environments and populations. The contributing factors are many and complex, and the biological data are too recent and unrefined to permit association of each cause with its specific effects or to understand synergistic effects of several factors acting in combination. It is against this background that efforts must be made to interpret the current ecological systems of the Mississippi-Alabama shelf and related coastal waters. Considering the rate of coastal habitat deterioration and population decline, the need to develop a comprehensive technical understanding of this complex system is most urgent.

#### ACKNOWLEDGMENTS

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# Gulf Research Reports

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## Long-Term Adult Population Fluctuations and Distribution of the Spot, *Leiostomus xanthurus*, in Mississippi

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# LONG-TERM ADULT POPULATION FLUCTUATIONS AND DISTRIBUTION OF THE SPOT, *LEIOSTOMUS XANTHURUS*, IN MISSISSIPPI

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**ABSTRACT** Adult specimens of the spot, *Leiostomus xanthurus*, were collected from bayou, Mississippi Sound, and barrier island locations along the Gulf Coast of Mississippi from November 1982 to July 1989. The mean total length of all spot sampled in comparable gill net sets was 219 mm ( $\pm 14$  standard deviation,  $n=4,338$ ). Ninety-five percent of the spot were collected in the island and sound areas, where the salinity was higher than in the bayous. Catch per unit effort was high at island and sound stations in spring and autumn, with relatively few fish caught during the winter spawning season and summer. The relatively high frequency of spot observed at the island stations in the autumn was probably influenced by spawning migrations, and the high spring values may represent a combination of two abundant year classes. The two greatest yearly collections, in 1983 and 1986, may have been influenced by sampling conditions or by environmental conditions favorable to survival either during those years or earlier when those fish were postlarvae. The smallest yearly catch occurred in 1985 and may have reflected the harsh weather conditions that year.

## INTRODUCTION

The spot, *Leiostomus xanthurus*, is a common fish in estuaries along the Gulf Coast of Mississippi. Several studies on the life history of this species have been conducted (e.g., Pearson 1929; Hildebrand and Schroder 1928; Hildebrand and Cable 1930; Dawson 1958; Parker 1971). Limited information is available on long-term population fluctuations. Kobylinski and Sheridan (1979) examined the long-term seasonal distribution and abundance of spot in Apalachicola Bay, Florida, and Joseph (1972) studied population trends along the mid-Atlantic Coast. Long-term monitoring of adult spot may indicate fluctuations in populations influenced by natural changes in the environment. The objectives of this study were to examine the seasonal and annual variation in catch rates of larger spot at island, sound, and bayou habitats in Mississippi in relation to temperature, salinity, and reproductive influences.

## MATERIALS AND METHODS

Spot samples and hydrological data were collected monthly from November 1982 through July 1989 at six stations along the Mississippi Gulf Coast (Figure 1). Specimens were collected with 183-m long by 2.4-m deep monofilament gill nets. The nets were comprised of four 45.7-m panels with 7.0, 9.5, 15.2, and 20.3-cm stretch mesh that were attached together. The net was set on the substratum perpendicular to the shore with the smallest mesh panel abutted to or near the shoreline. It was set in a

water depth of 0.5 to 3.0-m one hour before sunset and retrieved four hours later.

Spot were returned to the laboratory where total length (TL) and standard length (SL) were measured to the nearest millimeter. Representative samples were examined to determine the state of sexual maturity using methods similar to those established by Overstreet (1983). The date, water temperature, salinity, turbidity, cloud cover, and sea conditions were recorded prior to each net set. Water temperature was measured to the nearest 1°C with a hand-held thermometer. Salinity was measured to the nearest 1 ppt with a temperature-compensated refractometer or conductivity meter, and turbidity was measured with a secchi disk to the nearest cm. Most water temperatures and salinities were taken within 10 cm of the surface.

Three habitat types, represented by a total of six locations, were sampled from the study area (Figure 1). Bayou stations were located adjacent to Biloxi Bay near Fort Bayou and Popp's Ferry bridges. Sound stations were located off the north central portion of Deer Island and the northwest portion of Round Island. Island stations were located on the northcentral areas of Horn and Ship Islands.

A one-way analysis-of-variance test (ANOVA) was used to detect significant differences between mean values. In cases where differences were detected, means were compared using Tukey's multiple range test (Tukey 1953). Mean catch values in Figures 2 and 3 are presented as arithmetic means. The variance was proportional to mean values, hence  $\log_{10}$  transformations of data were performed prior to using the ANOVA and multiple range tests.

Linear regression was performed to compare the relationship between TL and SL in northern Gulf of Mexico spot to that calculated by Dawson in 1958 using South Carolina spot. Spot measured by the same biotechnician were compiled from a larger database consisting of spot we collected in the same geographical area as the data used for other statistical analyses performed in this study. The regression equation was calculated using the mean TL for a given SL to compare to Dawson's (1958) equation calculated from means of 5 mm class intervals.

## RESULTS

Gill nets selected larger spot; 96% of the specimens caught were greater than 200 mm TL (Table 1). Mesh sizes of 7.0, 9.5, 15.2, and 20.3 cm captured 95.3, 4.4, 0.2, and 0.1% of the spot, respectively, from the combination of bayou, sound, and island stations. Mean size of spot captured did not vary significantly among the bayou, sound, and island stations: 219 mm  $\pm$  16 (n=224), 221 mm  $\pm$  16 (n=1,382), and 219 mm  $\pm$  12 (n=2,732), respectively. The linear regression between TL and SL calculated for specimens from the northern Gulf of Mexico spot was  $TL=1.135[SL] + 14.2$ ,  $r^2=0.994$ .

Monthly mean catch rates of adult spot varied among bayou, sound, and island stations (Figure 2). A high percentage (63%) of the total catch occurred in the high-to-moderate salinities of the island stations, whereas 32% occurred in the moderate-salinities of the sound and 5% occurred in the lower-salinities of the bayou. Temperature and salinity varied among locations and seasons (Table 2), and correlation analysis indicated a weak but significant relationship between salinity and the number of spot caught ( $r=0.20$ , Table 3). A bimodal frequency of catch was evident because relatively large numbers of adult spot were collected at the island and sound stations in March-April and in October (Figure 2). Numbers of spot captured from the bayou stations were relatively low during each month throughout the study period. Although mean catch values among years were not significantly ( $p > 0.05$ ) different within each station, the total catch values from island and sound stations exhibited considerable annual variation, with especially large catches occurring in 1983 and 1986 (Figure 3).

Examination of spot gonads taken from bayou, sound, and island stations demonstrated that gravid females and ripe males occurred in all three habitats (Figure 4). Most of these individuals were observed from the island and sound stations in October and November. A low number of ripe males and gravid females, however, were collected from the bayou from October to December.

## DISCUSSION

Townsend (1956) examined the age-length relationship of spot in Florida using scales and length-frequencies, and he determined that spot between 150-185 mm SL ( $TL=187-230$  mm using the equation  $TL=1.233[SL] + 2$  from Dawson (1958)) were primarily age-2 fish. Parker (1971) determined that spot taken from the Gulf of Mexico grew approximately 11 mm per month during their first year and 5.5 mm per month during their second year. Consequently, these data would suggest that 220 mm TL fish were approximately 2.5 years old. Our data indicated 79% of the spot captured were between 190 and 229 mm TL and were probably 2 years old. Although our data represent length-frequency distribution skewed toward larger spot (190-331 mm TL), presumably in the 2- and 3-year age classes, we rarely observed individual spot larger than 250 mm TL. Only 66 out of 4,330 (1.5%) spot caught by gill net were larger than 255 mm. Gunter (1950) similarly noted only 2% of 1,246 spot longer than 255 mm TL captured by trawl along the Gulf Coast. Southeast Area Monitoring and Assessment Program (SEAMAP) data from 1982-1989 on spot captured from stations in Gulf of Mexico offshore waters bounded by 29°10' to 30°10'N latitude and 87°30' to 89°00'W longitude indicated only 1% of the 1,595 spot measured were larger than 255 mm (personal communication, Kenneth Savastano, National Marine Fisheries Service, NSTL, MS 39529 SEAMAP 1991). In addition, Dawson (1958) summarized catch data of spot collected by trawlers off the Atlantic Coast (Hildebrand and Schroder 1928; Hildebrand and Cable 1930) and reported 10 of 27,227 (0.04%)  $\geq$  255 mm TL. Our data from the Mississippi gill net study and those by others mentioned above demonstrate the infrequency of large spot in both estuarine and offshore areas, suggesting low survival of spot beyond 3 years of age.

Our TL/SL regression equation was not used because we did not have age data corresponding to that of Dawson (1958). Our regression equations and those of Dawson are more similar for smaller spot than larger ones and are probably not significantly different from each other in the 150-185 mm SL range. However, the lengths differ by more than 10 mm for fish greater than 220 mm SL.

Monthly variation in catch could have been influenced by migration, by short-term and long-term environmental variations, by spawning periods, and by sampling. Dawson (1958) noted the number of spot  $\geq$  150 mm TL in his samples from South Carolina was greater in March than in late spring. Those relatively small catches in late spring persisted until the start of autumn when the number increased (Dawson 1958). A similar trend was also observed in our study for adults sampled from the island and sound

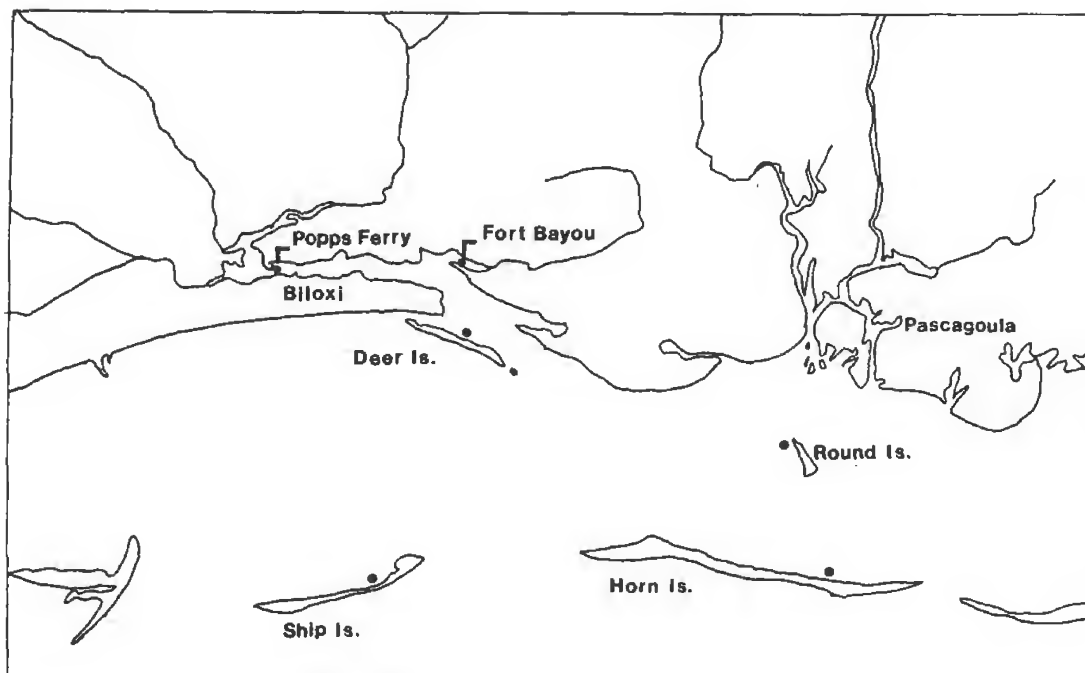


Figure 1. Locations of the six sampling areas in Mississippi: Popps Ferry, Fort Bayou, Deer Island, Round Island, Ship Island, and Horn Island.

stations in Mississippi. Hildebrand and Cable (1930) noted a comparable trend for juvenile spot from near Beaufort, North Carolina. The large number of adults we collected in October (Figure 2) may have resulted in part from a migration of the fish from inshore and coastal habitats to offshore spawning areas. Several studies have reported spawning migrations of spot during autumn based on large catches of adults from offshore spawning grounds relative to simultaneous small catches from inshore areas (Hildebrand and Schroder 1928; Pearson 1929; Gunter 1938, 1945; Dawson 1958). We corroborate that conclusion with similar observations (Figure 2).

Large numbers of migrating spot collected from the sound and island stations during late autumn had fully developed gonads. As expected from earlier reports (Gunter 1938, 1945; Dawson 1958), few spot were collected during December-February. Larger mean catches of spot from the island stations in March (mean=75) and April (mean=75) may have been influenced by the spent (spawned) or developing adults moving into and out of the area. These movements may have been triggered by gradual increases in water temperature in conjunction with consistent moderate-to-high salinities that occurred during those months. The relatively high number of spot observed for the seven-year period at the island stations during March and April were influenced by especially high catch rates in those

months in 1983, 1984, and 1986. Collections made in March of 1983 and 1986 accounted for 67% of the total seven-year catch for March, and 57% of the total number for April was caught in 1983 and 1984. A review of salinity and temperature data we collected each week during and a few months preceding the peak collection periods revealed no variations in conditions that would readily explain why the above periods were more productive than intermediate periods. Samples of a non-dispersed population during different conditions of water and air probably contributed to some of the variation. Perhaps favorable environmental conditions existed when these fish were larvae and postlarvae, contributing to the development of strong year classes. If data for the months of March 1983 and 1986 and April 1983 and 1984 were removed from the total data, the total number of occurrences for the months of March and April would not be significantly different ( $p > 0.05$ ) from those of May-September. The data indicate long-term stability of the spot population from March to September during the years 1983 to 1988.

Annual variation in the spot population is typical of a fish with a relatively short life cycle (Joseph 1972). Joseph also stated that population fluctuations could be influenced by survival of early stages, possibly resulting from environmental conditions that prevailed on the spawning grounds. However, detrimental conditions in the nursery grounds,



TABLE 2  
Mean salinity (ppt) and temperature (°C) of bayou, sound, and island stations by months — November 1982 to July 1989

| Month | N <sup>a</sup> | Bayou                   |             | Sound      |             | Island     |             |
|-------|----------------|-------------------------|-------------|------------|-------------|------------|-------------|
|       |                | Sal ± (SD) <sup>b</sup> | Temp ± (SD) | Sal ± (SD) | Temp ± (SD) | Sal ± (SD) | Temp ± (SD) |
| Jan   | 14             | 10 ± (4)                | 12 ± (3)    | 19 ± (8)   | 12 ± (3)    | 27 ± (4)   | 12 ± (3)    |
| Feb   | 14             | 3 ± (3)                 | 13 ± (3)    | 16 ± (7)   | 14 ± (3)    | 26 ± (6)   | 13 ± (4)    |
| Mar   | 14             | 4 ± (4)                 | 16 ± (2)    | 17 ± (6)   | 16 ± (2)    | 22 ± (6)   | 17 ± (3)    |
| Apr   | 14             | 3 ± (3)                 | 20 ± (2)    | 16 ± (6)   | 20 ± (2)    | 20 ± (5)   | 20 ± (3)    |
| May   | 14             | 6 ± (5)                 | 26 ± (2)    | 14 ± (8)   | 26 ± (3)    | 22 ± (7)   | 25 ± (2)    |
| Jun   | 14             | 3 ± (3)                 | 28 ± (3)    | 15 ± (6)   | 27 ± (2)    | 20 ± (7)   | 27 ± (2)    |
| Jul   | 14             | 6 ± (4)                 | 29 ± (2)    | 16 ± (7)   | 30 ± (2)    | 23 ± (4)   | 29 ± (1)    |
| Aug   | 12             | 3 ± (4)                 | 30 ± (2)    | 16 ± (7)   | 29 ± (2)    | 23 ± (5)   | 29 ± (2)    |
| Sep   | 12             | 6 ± (4)                 | 28 ± (3)    | 17 ± (7)   | 29 ± (2)    | 24 ± (5)   | 28 ± (3)    |
| Oct   | 12             | 9 ± (6)                 | 25 ± (3)    | 23 ± (5)   | 25 ± (3)    | 27 ± (5)   | 25 ± (3)    |
| Nov   | 14             | 13 ± (7)                | 22 ± (3)    | 22 ± (6)   | 20 ± (3)    | 29 ± (6)   | 20 ± (3)    |
| Dec   | 14             | 8 ± (7)                 | 15 ± (2)    | 20 ± (6)   | 16 ± (2)    | 26 ± (7)   | 17 ± (4)    |

<sup>a</sup>Number of samples measured per habitat

<sup>b</sup>Standard deviation

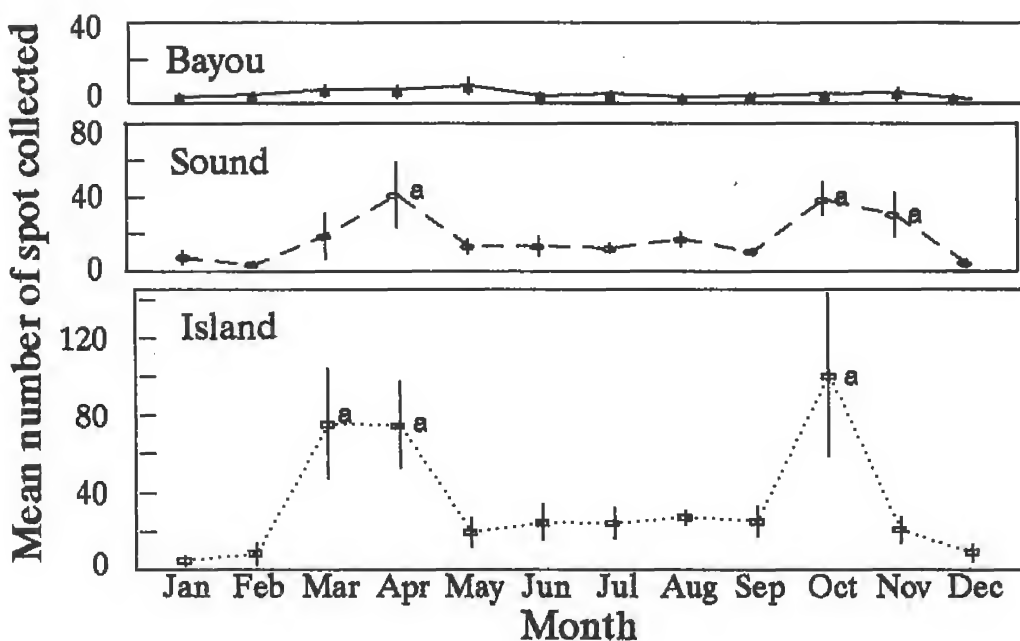


Figure 2. Mean number of adult spot by month from three sampling locations from November 1982 through July 1989. The letter "a" indicates a significant difference ( $p > 0.05$ ).

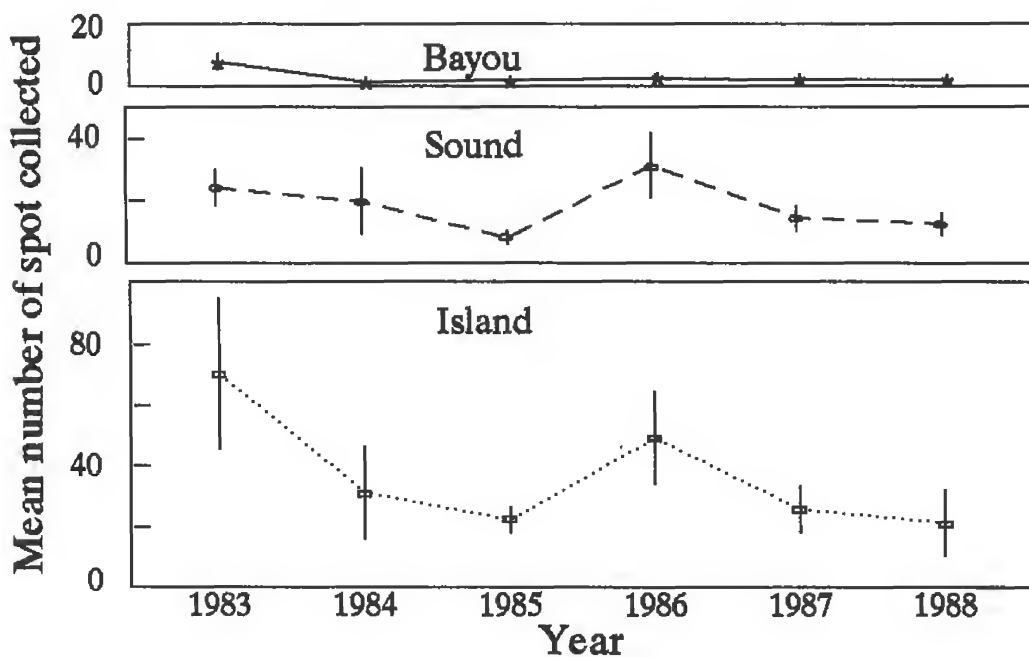


Figure 3. Mean number of adult spot by year from three sampling locations from 1983 through 1988.

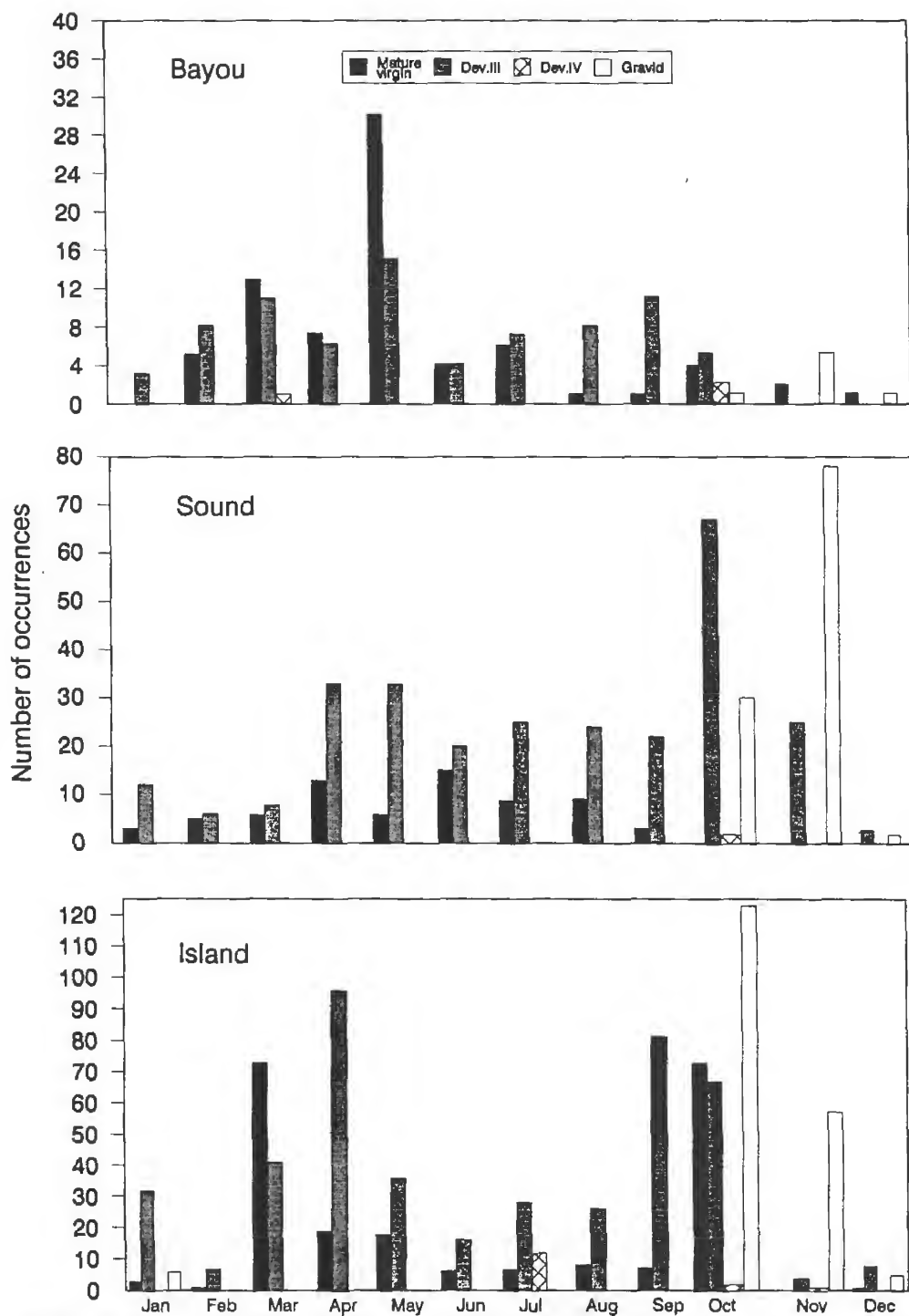


Figure 4. Number of occurrences of maturing virgins, developing, and gravid grouped male and female spot examined from bayou, sound, and island stations (see Table 1 of Overstreet, 1983 for explanation of developmental stages).

TABLE 3  
Correlation matrix for salinity, temperature, locality, and number of spot collected

|                 | Salinity | Temperature | Location | No. fish collected |
|-----------------|----------|-------------|----------|--------------------|
| Salinity        | —        | -0.07       | 0.74*    | 0.20*              |
| Temperature     | —        | —           | 0.003    | 0.03               |
| Locality        | —        | —           | —        | 0.32*              |
| Number of Cases | 492      |             |          |                    |

\*1-tailed significance .001

such as extended periods of low temperature, could also affect survival and migration of young spot into the bays during spring, subsequently effecting the strength of those yearclasses. For example, our collection of weekly weather data indicated that in January 1985, water temperature plunged from a mean of 10.3°C to a low of 2.5°C for at least 48 hours, with ice forming in many bayous. Also during that year, three hurricanes moved through the area. Those extreme weather conditions possibly dispersed or moved many adults into offshore waters in 1985 and negatively influenced survival of young fish in the bayous and sound. The lower total catch of adult spot seen in 1985 may be related to the harsh weather conditions occurring in that year. Moreover, the relatively low numbers of larger, adult

spot in 1987 and 1988 may also have been influenced by those same harsh conditions adversely effecting the survival of larvae or young-of-the-year fish during the winter of 1985.

#### ACKNOWLEDGMENTS

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Feeding Biology, Distribution, and Ecology of Two Species of Benthic Polychaetes:  
*Paraonis fulgens* and *Paraonis pygoenigmatica* (Polychaeta: Paraonidae)

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# FEEDING BIOLOGY, DISTRIBUTION, AND ECOLOGY OF TWO SPECIES OF BENTHIC POLYCHAETES: *PARAONIS FULGENS* AND *PARAONIS PYGOENIGMATICA* (POLYCHAETA: PARAONIDAE)

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**ABSTRACT** *Paraonis fulgens* and *Paraonis pygoenigmatica* inhabit sandy littoral and sublittoral sediments of the northern Gulf of Mexico and U.S. East Coast, but seldom overlap in distribution. The purpose of this study was to compare the feeding ecology and distribution of these species. We analyzed distributions and gut contents of Gulf of Mexico specimens and found that *P. fulgens* inhabited substrates with slightly more silt and clay than those inhabited by *P. pygoenigmatica*. Although *Paraonis fulgens* ingested more diatoms than *P. pygoenigmatica*, this distinction likely resulted from habitat differences, not selective feeding. Previous studies suggested that *P. fulgens* fed selectively on diatoms only.

## INTRODUCTION

The genus *Paraonis* Cerruti, 1909, contains just two species, *Paraonis fulgens* and *Paraonis pygoenigmatica*. *Paraonis fulgens* is distributed worldwide in shallow estuarine and marine habitats (Strelzov 1973). However, *P. pygoenigmatica* occurs only in coastal waters of the U.S. Atlantic (Jones 1968) and northern Gulf of Mexico (Gaston 1984). Both species inhabit sandy substrates; *P. fulgens* generally inhabits littoral and sublittoral sediments and *P. pygoenigmatica* lives in slightly deeper water. Apparently, only *P. fulgens* occurs in dense populations (Gaston 1984). Roder (1971) and Risk and Tunnicliffe (1978) reported that *P. fulgens* fed solely on diatoms, but little else is known about the feeding ecology of these species.

The purpose of this study was to compare the feeding ecology and distribution of these two species in northern Gulf of Mexico habitats. We investigated ingested foods to determine if differences in food accounted for their distinct distributions.

## MATERIALS AND METHODS

Most of the specimens examined for this study were collected by Gulf Coast Research Laboratory (GCRL) personnel off Biloxi, Mississippi, Ship and Horn Island, Mississippi and Perdido Key, Florida (Rakocinski et al. 1991, McLelland and Heard 1991). Additional specimens were collected as part of a Bureau of Land Management (now Minerals Management Service) Gulf of Mexico Outer Continental Shelf baseline study conducted during 1975-1981 (Uebelacker and Johnson 1984); along the Florida Gulf Coast by Mote Marine Laboratory personnel; off Padre Island, Texas (Rabalais and Flint 1983); in Pelican Bay, Alabama during the EPA Environmental Monitoring

and Assessment Program (EMAP); and off Alabama, Texas, and the Middle Atlantic Bight by the author (Gaston 1985, 1987).

Percentage of ingested food was estimated under compound microscopy as percentage represented by diatoms (estimated volume) versus percentage represented by detritus. None of the guts examined were entirely empty. Statistical analyses involved a T-test for significant differences ( $\alpha = 0.05$ ) between species (when the Bartlett Test indicated homogeneity of variables) using arcsine-transformed percentage data (percentage of food represented by diatoms).

## RESULTS AND DISCUSSION

Both *P. fulgens* and *P. pygoenigmatica* inhabited sandy substrates with similar sediment characteristics (Table 1). *Paraonis fulgens* was most abundant in sandy intertidal and shallow subtidal habitats with 96-99% sand (i.e., less than 4% silt and clay) as indicated in Table 2. *Paraonis pygoenigmatica* inhabited slightly deeper-water habitats with 2-3% silt and clay (Tables 1 and 2).

*Paraonis fulgens* was one of the most abundant macrobenthic organisms collected in the shallow waters off Perdido Key, Florida and Horn and Ship Islands, Mississippi. Their numbers peaked at both Ship Island and Horn Island during August 1990 at over 10,000/m<sup>2</sup> (Table 1). Colonization of the sediments by settling juveniles apparently occurred during summer. *Paraonis pygoenigmatica* was seldom as abundant as *P. fulgens* (Table 1). It occurred from subtidal to outer continental shelf waters, and seldom was collected at the same sites as *P. fulgens* (Table 1). In Perdido Key, *P. fulgens* inhabited sandy sediments between the beach and sand bar just offshore (0 - 5.5m) and *P. pygoenigmatica* occurred beyond the sand bar (5.5 - 5.8m) as shown in Table 2.

TABLE 1

Selected distribution records and population densities of *Paraonis fulgens* and *Paraonis pygoenigmatica* in the Gulf of Mexico and southern Florida Atlantic Coast. Depths in meters.

| Site                           | Depth(s)  | Sediments | Density/m <sup>2</sup> | Source               |
|--------------------------------|-----------|-----------|------------------------|----------------------|
| <i>Paraonis fulgens</i>        |           |           |                        |                      |
| Horn Island, MS                | <1.0–30.0 | >97% sand | 1500–10,000            | GCRL *               |
| Ship Island, MS                | 15.0–30.0 | >96% sand | 2000–12,000            | GCRL *               |
| Biloxi Bay, MS                 | 0.1–0.2   | sand      | <500                   | Matulewski **        |
| Pelican Bay, AL                | 2.4       | sand      | <10                    | Gaston **            |
| Mobile Bay, AL                 | 2.4–3.6   | sand      | 20–800                 | Gaston **            |
| Mobile Bay, AL                 | 4.0–6.5   | sand      | <500                   | Johnson 1980         |
| Perdido Key, FL                | 1.0–5.5   | sand **   | 500–8000               | GCRL *               |
| FL Continental Shelf           | 19.0–20.0 | fine sand | <10                    | Gaston 1984          |
| Marco Island, FL               | 0.5–1.0   | sand      | <50                    | Milligan **          |
| Padre Island, TX               | 0.1–2.0   | fine sand | mean = 200             | Rabalais et al. 1983 |
| <i>Paraonis pygoenigmatica</i> |           |           |                        |                      |
| Ft. Lauderdale, FL             | 10.0      | sand      |                        | Milligan **          |
| Perdido Key, FL                | 1.0–5.5   | sand ***  | <50                    | GCRL *               |
| off Tampa, FL                  | 20.0–24.0 | fine sand | 10–60                  | Gaston 1984          |

\* Data from two Gulf Coast Research Laboratory studies (McLelland and Heard, 1991; Rakocinski et al. 1991).

\*\* Unpublished data: K. Matulewski (University of Southern Mississippi), G. Gaston (University of Mississippi), M. Milligan and A. McAllister (Mote Marine Laboratory), EMAP-NC 1991 Gulf of Mexico estuary survey.

\*\*\* See Table 2 for more sediment data.

*Paraonis fulgens* is a subsurface detritivore. It feeds in tight spirals beneath the sediment surface, and moves upward or downward as it completes a feeding spiral (Risk and Tunnicliffe 1978). Previous research indicated that *P. fulgens* selectively ingested benthic diatoms (Roder 1971, Risk and Tunnicliffe 1978), whereas other paraonids feed on drift debris or detritus and are probably non-selective (Fauchald and Jumars 1979, Gaston 1983). Roder (1971) noted that specimens he examined contained no detritus,

only diatoms. Although diatoms were ingested by many specimens that we examined (Table 3), diatoms were apparently ingested passively with other detritus. Most of our specimens were filled with detritus, which included a few dinoflagellate and diatom tests. It did not appear that diatoms and/or dinoflagellates were selectively ingested; most ingested diatoms were small, unlike those observed by Roder (1971), and there were several diatom species represented. Furthermore, diatoms seldom composed even

TABLE 2

Habitat and sediment characteristics of sites where *Paraonis fulgens* (P.f.) and *Paraonis pygoenigmatica* (P.p.) were collected at Perdido Key, Florida. Abundances: C = Common ( $>1000 \text{ m}^{-2}$ ); R = Rare ( $<20 \text{ m}^{-2}$ ). From Rakocinski et al. (unpublished data).

| Station           | Abundance<br>P.f. / P.p. | Depth (m) | % Sand<br>(md. dia) | % Silt/clay |
|-------------------|--------------------------|-----------|---------------------|-------------|
| 1. Littoral *     | C -                      | 1.0       | 98.8 (0.29)         | 1.2         |
| 2. Littoral       | C -                      | 2.0       | 99.6 (0.25)         | 0.4         |
| 3. Longshore bar  | C -                      | 1.0       | 98.9 (0.21)         | 1.1         |
| 4. Sublittoral ** | C -                      | 2.1       | 99.6 (0.20)         | 0.4         |
| 5. Sublittoral    | C -                      | 3.7       | 98.6 (0.20)         | 1.4         |
| 6. Sublittoral    | C -                      | 4.3       | 98.7 (0.28)         | 1.3         |
| 7. Sublittoral    | C R                      | 5.5       | 99.5 (0.30)         | 0.5         |
| 8. Sublittoral    | - R                      | 5.5       | 99.7 (0.32)         | 0.3         |
| 9. Sublittoral    | - R                      | 5.5       | 97.4 (0.28)         | 2.6         |
| 10. Sublittoral   | - R                      | 5.5       | 96.7 (0.25)         | 3.3         |
| 11. Sublittoral   | - R                      | 5.8       | 97.7 (0.24)         | 2.3         |

\* Littoral = between beach and longshore bar.

\*\* Sublittoral = outside the longshore bar.

half of the matter ingested (Table 3), and many lacked chlorophyll, indicating that they were probably empty frustules when ingested.

Like many paraonids, *P. pygoenigmatica* is a subsurface detritivore (Fauchald and Jumars 1979, Gaston 1983). It is less commonly collected than *P. fulgens*, as evidenced by the few numbers of specimens on Table 3. Whether or not it feeds in spirals is unknown. Gut contents of specimens collected in Perdido Key and in the Middle Atlantic Bight were filled with detritus, but included fewer diatoms than were ingested by *P. fulgens* ( $P < 0.01$ , Table 3).

These two species of *Paraonis* are members of the sandy littoral and sublittoral communities of the Atlantic and Gulf of Mexico. Their communities were numerically dominated by crustaceans in the northern Gulf; off West Ship Island, Mississippi the dominant taxa were an amphipod (*Lepidactylus* sp.), an isopod (*Exosphaeroma diminutum*), a cumacean (*Spilocuma watlingi*), two polychaetes

(*P. fulgens* and *Dispio uncinata*), and a tanaid (*Kalliapseudes* sp.) (Rakocinski et al. 1991). A similar trophic group dominated their communities off Mobile Bay, Alabama and Perdido Key, Florida, including haustoriid amphipods, the isopod (*E. diminutum*), and the same polychaetes (Gaston 1986, Rakocinski et al., manuscript). These dominants were collected in habitats of both species of *Paraonis* at Perdido Key, even though *P. fulgens* and *P. pygoenigmatica* seldom were collected together (Table 2).

The sediments where *P. fulgens* was most abundant were more dynamic than those inhabited by *P. pygoenigmatica*. Perhaps more diatoms were buried in the dynamic sediments and became detritus for grazing *P. fulgens*, as suggested by Risk and Tunnicliffe (1978). Unfortunately, the environmental and gut-contents data provided little additional information on the distinction of the habitats of these two species. Apparently, *P. fulgens* feeds on detritus that includes diatoms, but *P. pygoenigmatica* does not.

TABLE 3

Gut-contents data of two species of *Paraonis* from three locations in the Gulf of Mexico. Percentage values are percent volume, estimated to the nearest 5%. Specimens collected in different samples are presented as separate data.

| Site                     | Number examined | % Diatoms | % Detritus |
|--------------------------|-----------------|-----------|------------|
| <i>P. fulgens</i>        |                 |           |            |
| Horn Island, MS          | 6               | 10        | 90         |
| Horn Island, MS          | 2               | 25        | 75         |
| Horn Island, MS          | 1               | 50        | 50         |
| Perdido Key, FL          | 2               | <5        | 95         |
| Perdido Key, FL          | 4               | 10        | 90         |
| Perdido Key, FL          | 7               | 25        | 75         |
| Perdido Key, FL          | 4               | 50        | 50         |
| Pelican Bay, AL          | 1               | <5        | 95         |
| Totals/Mean              | 27              | 21.1      | 78.9       |
| <i>P. pygoenigmatica</i> |                 |           |            |
| Perdido Key, FL          | 10              | <5        | >95        |
| off Tampa, FL            | 2               | 0         | 100        |
| Totals/Mean              | 12              | 1.6       | 98.4       |

Thus, even though these two species are closely related, their feeding biology is distinct. We propose that dissimilar habitats, and the abundance of diatoms in those habitats, account for their distinctive feeding biology. *P. fulgens* forages for detritus (which may be diatom-laden detritus) in dynamic sediments of littoral and sublittoral zones, while *P. pygoenigmatica* is associated with less diatomaceous detritus in lower energy habitats beyond the swash zone.

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## Closed System Culture of *Penaeus vannamei*

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## CLOSED SYSTEM CULTURE OF *PENAEUS VANNAMEI*

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**ABSTRACT** *Penaeus vannamei* were cultured utilizing three different closed recirculating seawater systems. The first system used biological filtration for water treatment. The second system utilized both physical and chemical filtration, but no biological filtration. The third system used a combination of biological, physical, and chemical filtration. Shrimp growth was monitored for a 12-week period for each system. Shrimp from the biological filtration system had a growth rate of 0.82 g/wk and an overall survival rate of 45.6%. Shrimp from the closed system which used physical and chemical filtration had a growth rate of 0.99 g/wk and a survival rate of 29.2%. In the third system which combined both types of filtration, the shrimp growth rate averaged 0.65 g/wk and the survival rate was 56.9%.

### INTRODUCTION

The intensive culture of marine shrimp has been of interest since shrimp farming first began in the late 1960s. Initial grow-out trials at the Bureau of Commercial Fisheries in Galveston, Texas began in raceway tanks in 1972 and continued into 1980. One commercial venture, Intensive Culture Systems (Summerland Keys, Florida), attempted to grow shrimp in intensive closed systems as early as 1974. One of the largest attempts at closed system marine shrimp culture was by Aquabiotics (King James, Inc., Park Forrest, Illinois) in 1979. Currently, there are at least three commercial ventures working with closed systems for the culture of marine shrimp: the Stillman Ranch and Red Ewald in Texas, and Aquamar in Florida. Two research facilities, the University of Texas Marine Science Institute (Port Aransas, Texas) and the Gulf Coast Research Laboratory (Ocean Springs, Mississippi) are researching closed system culture on a small scale.

### MATERIALS AND METHODS

Three grow-out trials were conducted during 1989. The first two trials were run simultaneously and shrimp growth in the two unreplicated systems was compared. Shrimp system 1 (SS-1) utilized biological filtration, while shrimp system 2 (SS-2a) utilized both physical and chemical filtration with no biological filtration. The third trial, shrimp system 3 (SS-3a), utilized a combination of biological, physical and chemical water treatment. All systems were housed in a passively-heated greenhouse.

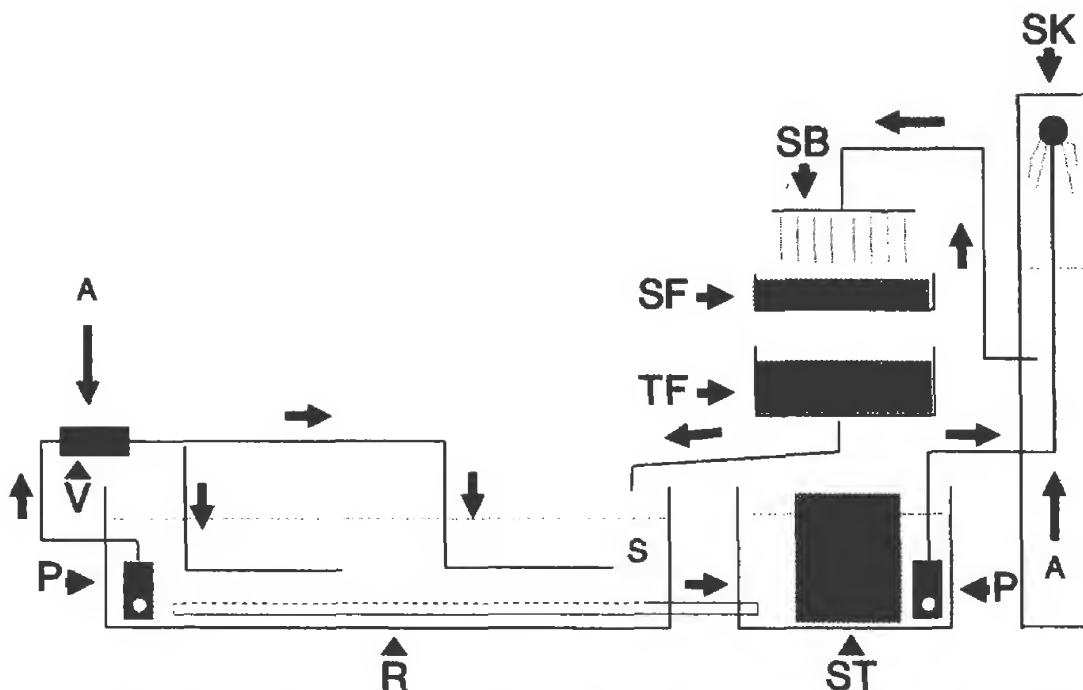
**Shrimp System 1.** SS-1 (Fig. 1) consisted of a 1.8 m x 7.3 m x 0.28 m rectangular raceway with an area of 13.28 m<sup>2</sup> and a volume of 5.74 m<sup>3</sup>. Wastewater was collected in

a 5.08 cm diameter PVC slotted pipe running the length of the tank and passed by gravity flow through the end wall into a settling tank. The settling tank, 0.93 m x 1.85 m x 0.61 m, was packed with a plastic media, Norpac (Jaeger Products, Inc., Spring, Texas). A chamber at one end provided room for a submersible sump pump (Little Giant 6C1, MR #506913, Oklahoma City, Oklahoma) which supplied water through a 3.81 cm PVC pipe split into three distribution pipes. Two of the pipes were plumbed into the top of a pair of protein skimmers, 0.15 m in diameter and 1.8 m high, sparged with compressed air. Water exited the bottom of the skimmers and was elevated by gravity to two rotating spray bars. Water from the spray bars irrigated two aerobic trickling filters.

The filters were constructed of a synthetic spawning mat material (Anderson Bait Company, Lonoke, Arkansas) wound in a spiral around corrugated fiberglass panels which rested on top of a biological filter. Effluent from the spiral filters trickled into the top of the submerged trickling biological filter. The biological filter was constructed in a 0.96 m x 1.9 m x 0.2 m fiberglass tank. Plastic egg crate louvers suspended off the tank bottom with 2.54 cm diameter PVC pipe served as a support for clam shell and a media of ground PVC. Water flowed down through the media and out a bottom drain into the raceway. A 5.1 cm diameter PVC standpipe maintained water in the submerged trickling biofilter at a depth of 17.8 cm. The third pipe from the pump was directed to a spray bar running the length of the raceway and suspended above the water.

Additional circulation was provided by a ½ hp Jacuzzi pump (Model 5L, Little Rock, Arkansas). The intake pipe was placed inside a circular basket perforated with 1.27 cm square holes and covered with screen. The basket was used to prevent shrimp from being aspirated by the pump. Water passed through the basket into a submerged 2.54 cm diameter spray pipe running the length of the raceway. A venturi injector (Sophisticated Systems, Palm Harbor, Florida)

(Use of trade names does not imply endorsement.)



**Figure 1.** Cross-section diagram of SS-1 utilizing biological filtration: P - pump, V - venturi injector, R - raceway, ST - settling tank, TK - trickling filter, SF - spiral filter, SB - spray bar, SK - skimmer, A - site of air injection, S - site of sample collection.

was installed in the supply pipe to oxygenate the water. Total area of the system including filters was 16.9 m<sup>2</sup> and total volume was 6.6 m<sup>3</sup>. Ten net substrates, 30.5 cm x 152 cm with 0.6 cm mesh openings, were secured across the culture tank to provide shelter. Water flow for SS-1 was 28 gpm with a turnover rate of 23 times per day (Table 1).

In week 11, water lost throughout the study was replaced (80% water change) and the system was cleaned.

**Shrimp System 2a.** A rectangular raceway, 1.8 m x 7.3 m x 0.6 m, a lamellar separator and reservoir box containing six protein skimmers were the main components of SS-2a (Fig. 2). A 7.6 cm slotted PVC pipe running the length of the raceway collected wastewater. The water was pumped (Little Giant, 6CI MR #506913, Oklahoma City, Oklahoma) into the bottom of a lamellar separator inside a 0.76 m x 2.1 m x 0.91 m tank elevated 0.2 m above the floor. Water flowed up through the angled lamellar media and cascaded into the reservoir box, 1.0 m x 0.91 m x 1.3 m, which contained the six protein skimmers.

The protein skimmers were constructed of PVC pipe 10.1 cm in diameter and 1.6 m in length. A 2.54 cm hole located 1.1 m from the bottom of the skimmer allowed

water to flow into the skimmer pipe. Water flowed out the bottom of the skimmer through a 5.08 cm diameter PVC pipe connected to a manifold constructed of 30.48 cm PVC pipe. A 5.08 cm diameter PVC pipe in one end of the manifold connected through the sidewall of the reservoir box to the intake of a Jacuzzi ½ hp pump (Model 5L, Little Rock, Arkansas). Water was directed through a venturi aspirator (Sophisticated Systems, Palm Harbor, Florida) into a submerged spray bar running the length of the raceway. Activated air (ozone) generated from a UV unit (Water Management, Inc., Pascagoula, Mississippi) was sparged into the six protein skimmers and injected into the venturi. Ten 1.5 m x 0.30 m nets were hung vertically across the culture tank to provide additional substrate for shrimp. Water flow for SS-2a was 32 gpm with a turnover rate of 20 times per day. The system had a total area of 13.5 m<sup>2</sup> and a total volume of 8.7 m<sup>3</sup>.

**Shrimp System 3a.** SS-3a was constructed later in 1989 by utilizing some components from the other two systems as noted. The system consisted of four circular tanks, 1.8 m in diameter, 66.0 cm in depth with a capacity of 2,273 L each (Fig. 3). A screened standpipe allowed

TABLE 1  
Physical and biological parameters for three closed systems.

| System               | SS-1  | SS-2a | SS-3a |
|----------------------|-------|-------|-------|
| Area                 |       |       |       |
| total m <sup>2</sup> | 16.9  | 13.5  | 12.2  |
| filter %             | 21.3  | 11.9  | 14.9  |
| ratio f/t*           | 0.27  | 0.13  | 0.17  |
| Volume               |       |       |       |
| total m <sup>3</sup> | 6.6   | 8.7   | 10.1  |
| gallons              | 1752  | 2303  | 2767  |
| filter %             | 13.5  | 30.5  | 33.1  |
| ratio f/t*           | 0.15  | 0.44  | 0.49  |
| Water                |       |       |       |
| flow (gpm)           | 28    | 32    | 24    |
| turnover/day         | 23    | 20    | 13    |
| exchange %/wk        | 7.1   | 1.8   | 3.3   |
| Stocking             |       |       |       |
| number               | 3300  | 3300  | 4480  |
| tank                 |       |       |       |
| #/m <sup>2</sup>     | 248   | 277   | 430   |
| #/m <sup>3</sup>     | 575   | 500   | 663   |
| system               |       |       |       |
| #/m <sup>2</sup>     | 195   | 244   | 367   |
| #/m <sup>3</sup>     | 497   | 378   | 444   |
| Harvest 12 wk        |       |       |       |
| mean size (g)        | 11.60 | 13.02 | 8.09  |
| growth g/wk          | 0.82  | 1.00  | 0.65  |
| survival %           | 45.6  | 29.2  | 56.9  |
| production kg        | 12.5  | 17.4  | 20.7  |
| kg/m <sup>3</sup>    | 1.9   | 2.0   | 2.0   |
| gal/lb               | 118   | 73    | 88    |

\*ratio of filter to tank

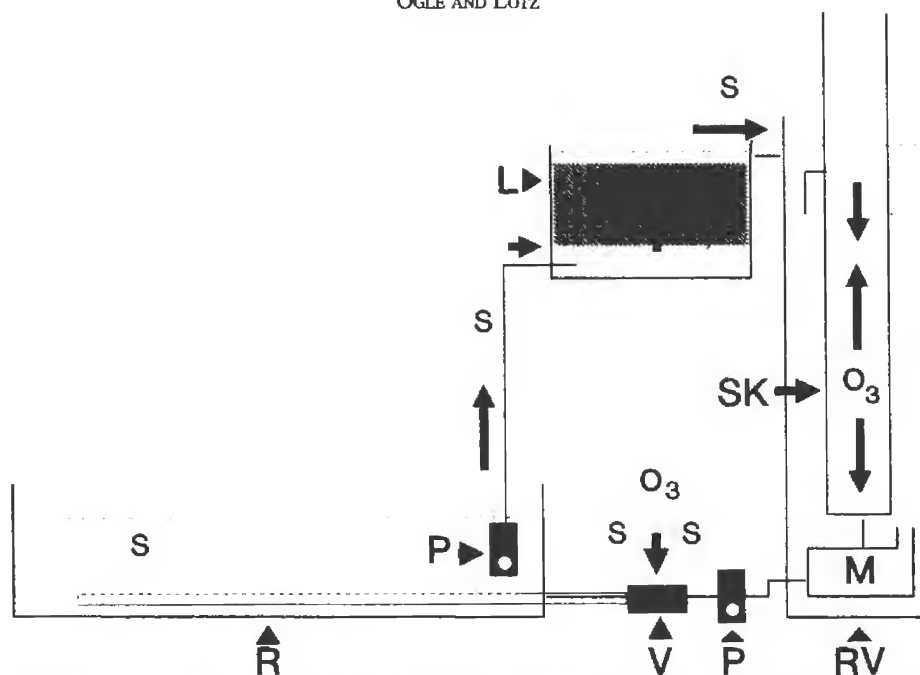


Figure 2. A cross-section diagram of SS-2a utilizing chemical and physical water treatment: R - raceway, P - pump, V - venturi injector, L - lamellar separator, SK - skimmer, RV - reservoir tank, O - site of ozone injection, S - site of sample collection.

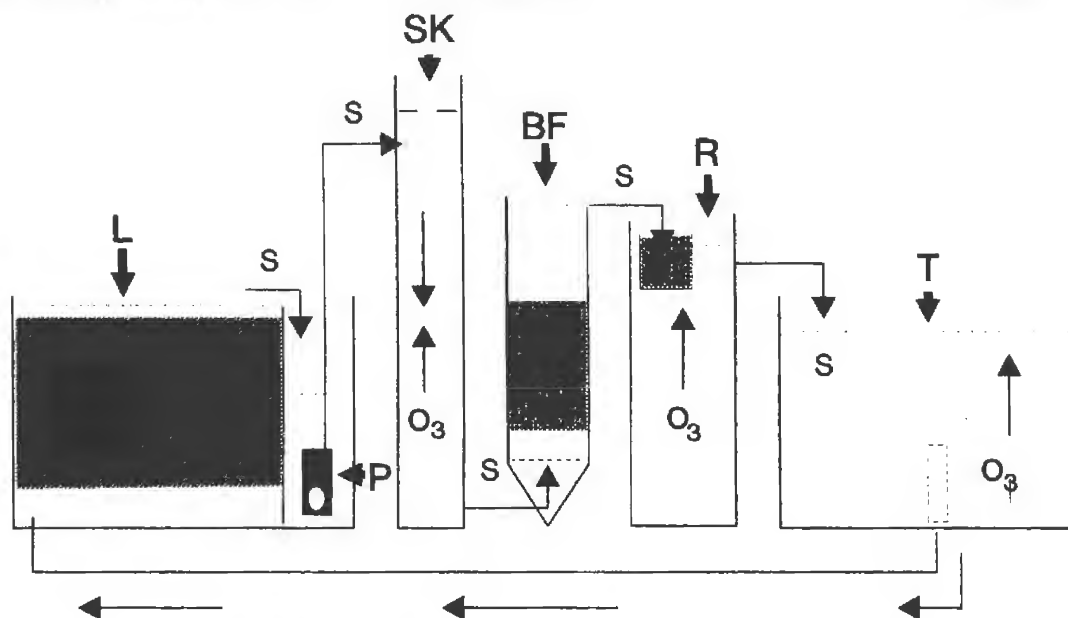


Figure 3. A cross-section diagram of SS-3a utilizing chemical, physical and biological water treatments: L - lamellar separator, P - pump, SK - skimmer, BF - biological filter, R - reservoir tank, T - culture tank, O - site of ozone injection, S - site of sample collection.

water to flow out of the tanks through 5.08 cm center drains where it was directed to the bottom of the lamellar separator used in SS-2a. Water flowed up the inclined media of the separator and overflowed into a pump chamber. The pump chamber, a 81.3 cm x 71.1 cm x 81.3 cm fiberglass tank, had a 3.81 cm PVC bulkhead fitting in the sidewall which connected directly to a ½ hp Jacuzzi pump.

The pump supplied water to the top of a 30.5 cm diameter, 2.4 m tall tank with a conical insert having a 5.08 cm center hole, all of which served as a protein skimmer. Water exited the bottom of the skimmer and entered the bottom of a biofilter. The biofilter was constructed of a conical-bottomed 0.029 m cylindrical tank 1.5 m tall. A diffusor plate with holes on 2.54 cm centers was placed at the top of the conical part of the filter tank. Gravel placed on top of the diffusor retained the carbon used as a filter media. Water flowed up through the filter, which caused some fluidization, where it was collected in an overflow trough and directed to a reservoir chamber used in SS-2a. Water entering the reservoir flowed through a cylindrical plastic perforated basket used in SS-1 containing a bonded filter matting (Fritz Aquaculture, Dallas, Texas). Four separate bulkhead fittings exited the sidewall of the reservoir and directed the water back to the culture tanks.

Flow rates were controlled by valves. Excess water from the reservoir was directed by an overflow pipe back to the pump chamber. Ozone was sparged into the skimmer, the reservoir and directly into each of the four culture tanks. Total area for SS-3a was 12.2 m<sup>2</sup> and total volume was 10.1 m<sup>3</sup>. The flow rate was 24 gpm with a turnover rate of 13 times per day.

Hatchery-reared *Penaeus vannamei* postlarvae, cultured to a minimum size of 1 g, were hand counted into the three systems. SS-1 and SS-2a were stocked in February 1989 with 3,300 shrimp each. SS-3a was stocked in August 1989 with 1,140 shrimp per tank for a total of 4,480 shrimp. Salinity varied from 16 to 20 ppt and temperature ranged from 23 to 28°C.

Shrimp were fed continuously utilizing automatic Zeigler baby belt feeders (Gardners, Pennsylvania). Rangen (Buhl, Idaho) and Zeigler (Gardners, Pennsylvania) artificial shrimp grower feeds were fed to shrimp at a rate of 5% body weight. A sample of no less than 25 animals were individually weighed each week to the nearest 0.01 g on an electronic balance. Feeding rates were adjusted weekly for all systems. Shrimp growth was monitored for a period of 12 weeks, at which time tanks were harvested and survival rates determined. Water quality values for pH and ammonia were determined weekly by using an Orion pH/ion analyzer. Nitrite and nitrate were determined by standard methods (EPA 1983) each week. Sodium carbonate was added as needed in an attempt to regulate pH. Water was added only to replace loss and after occasional flushing of the lamellar separator. In addition, total heterotrophic

bacteria were determined by plating on marine agar and counting colony-forming units. Presumptive *Vibrio* colony-forming units cultured on TCBS agar were counted weekly for SS-1 and SS-2a. Additional weekly water quality samples were taken from the inflow and outflow for each filter component of SS-2a and SS-3a for three weeks prior to the 12-week inventory. After the systems were modified, additional samples were taken for three weeks prior to the 20th-week harvest. The difference between values for inflow and outflow for each component was calculated and expressed as percent instantaneous change for ammonia and for nitrate.

After the 12-week period when shrimp were harvested, SS-2a and SS-3a were modified and labelled as SS-2b and SS-3b, respectively. Additional water quality samples were analyzed from the individual filter components.

For SS-2b, six 0.16 m<sup>2</sup>, 1.5 m high skimmers were plumbed directly into the lamellar outflow (Fig. 4). Water flowed down through the skimmers, out the bottom and was directed back up over the side of the reservoir chamber. SS-3b (Fig. 5) was modified by addition of a hydrocyclone (Flo Trend Systems, Inc, Denton, Texas) for particulate removal. The hydrocyclone was plumbed inline between the pump and the skimmer. The 30.48 cm diameter skimmer was replaced with a 45.72 cm diameter cylinder. The biofilter was replaced with a flat bottomed cylinder with a conical top 61 cm in diameter. Water exited the top of the filter through a 5.08 cm diameter PVC pipe which directed the water through the sidewall of the reservoir.

## RESULTS

Results for the three systems were significantly different. Shrimp growth averaged 0.82, 0.99 and 0.65 g/wk and survival rates for the 12-week period were 45.6%, 29.2% and 56.9% for SS-1, SS-2a and SS-3a, respectively. Total production was 12.5, 17.4 and 20.7 kg or 1.9, 2.0, and 2.0 kg/m<sup>3</sup> for SS-1, SS-2a and SS-3a, respectively (Table 1). Water varied in pH from 7.12 to 7.87 for SS-1, 7.22 to 7.93 for SS-2a, and 7.33 to 7.80 for SS-3a (Fig. 6). Total ammonia fluctuated from 0.01 to 0.254 ppm for SS-1, 0.094 to 0.455 ppm for SS-2a, and 0.083 to 1.06 ppm for SS-3a (Fig. 7). Nitrite fluctuated from 0.098 to 2.12 ppm for SS-1, 0.074 to 2.35 ppm for SS-2a, and 0.063 to 1.38 ppm for SS-3a (Fig. 8). Nitrate increased from 0.118 to 55.3 ppm for SS-1, varied between 1.35 to 23.6 ppm for SS-2a, and ranged from 4.79 to 12.5 ppm for SS-3a (Fig. 9). Nitrate was actually reduced in SS-2a and SS-3a. A comparison was made of the water quality data for systems 2a, 2b, 3a and 3b for the individual filter components. The pump removed ammonia from all systems ranging from 3.2% to 13.5%. The lamellar separator was also removing ammonia except in SS-3a where ammonia was added. The skimmer for SS-2a and 2b also increased the ammonia

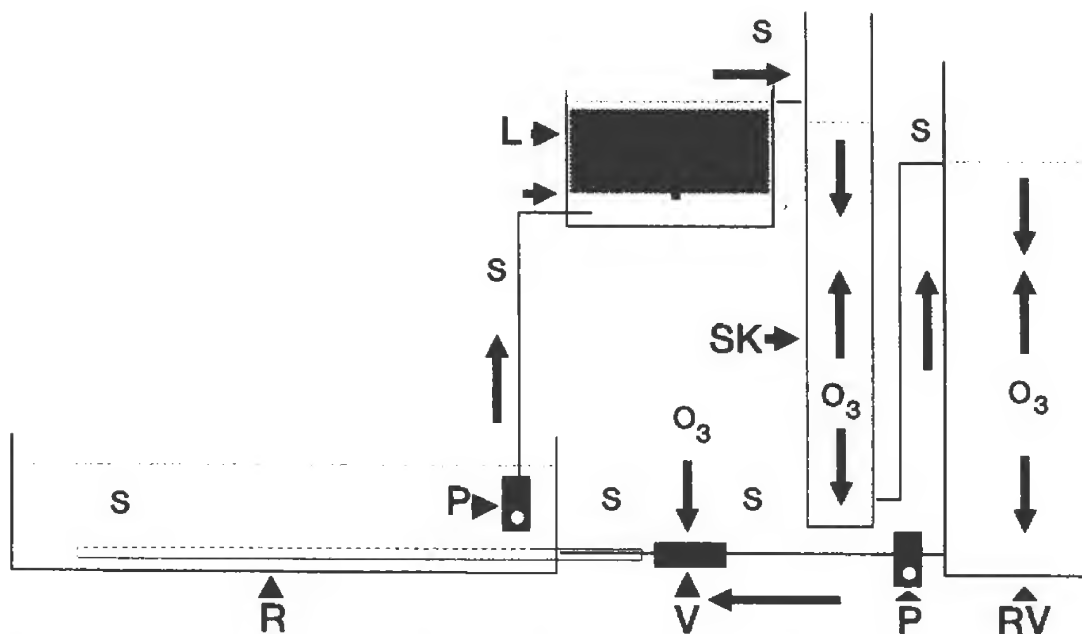


Figure 4. A cross-section diagram of SS-2b after modification: R - raceway, P - pump, L - lamellar separator, SK - skimmer, RV - reservoir tank, V - venturi injector, O - site of ozone injection, S - site of sample collection.

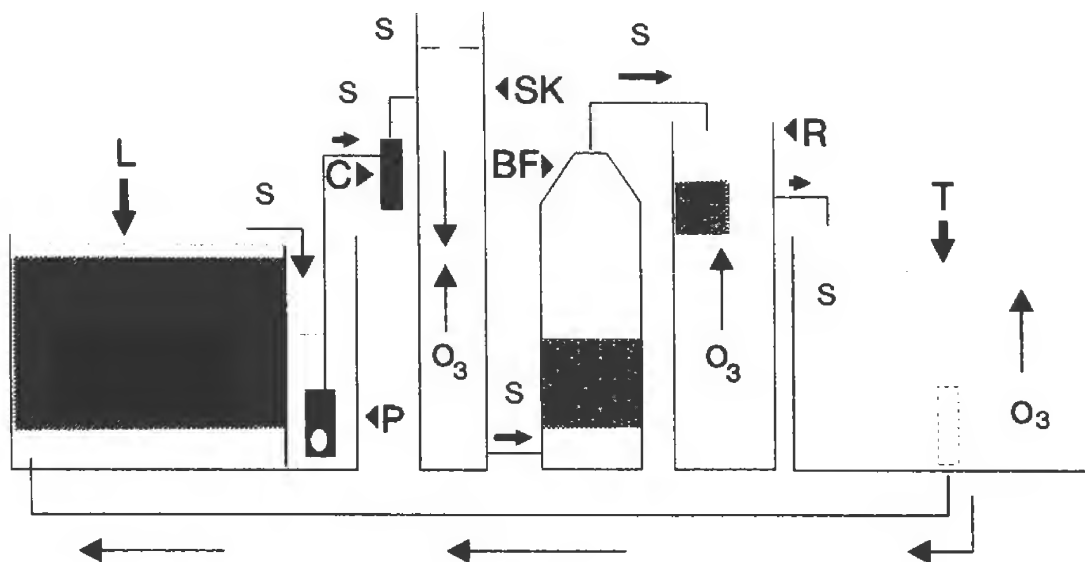


Figure 5. A cross-section diagram of SS-3b after modification: L - lamellar separator, P - pump, C - hydrocyclone particle separator, SK - skimmer, BF - biological filter, R - reservoir tank, T - culture tank, O - site of ozone injection, S - site of sample collection.

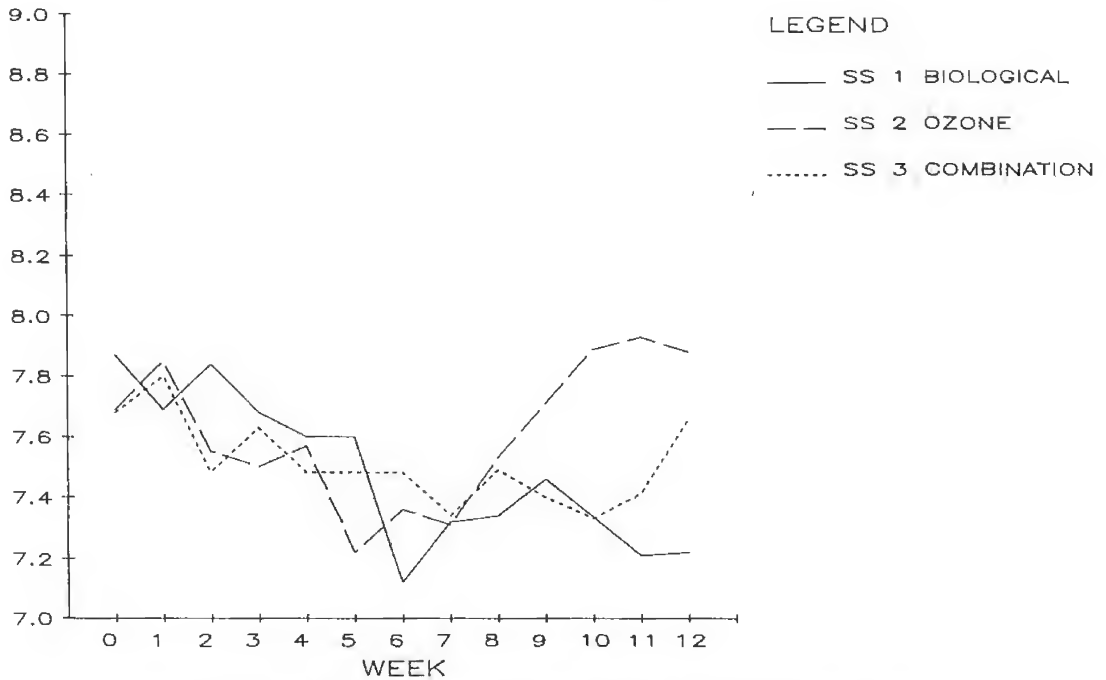


Figure 6. Graph of pH monitored over a 12-week period for three shrimp systems.

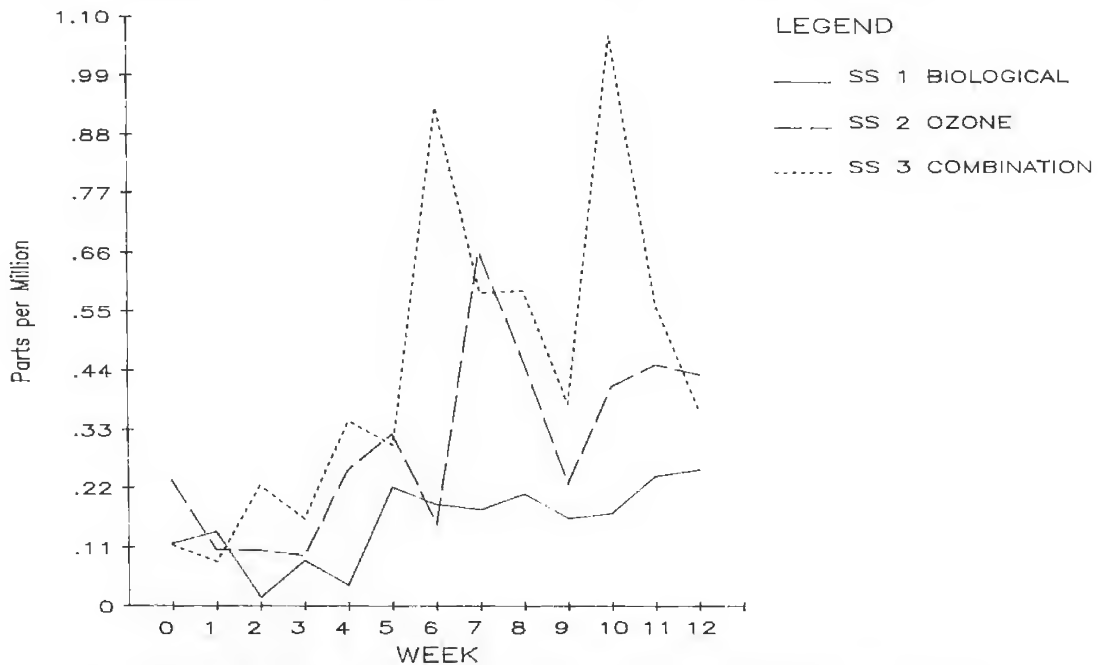


Figure 7. Graph of total ammonia monitored over a 12-week period for three shrimp systems.

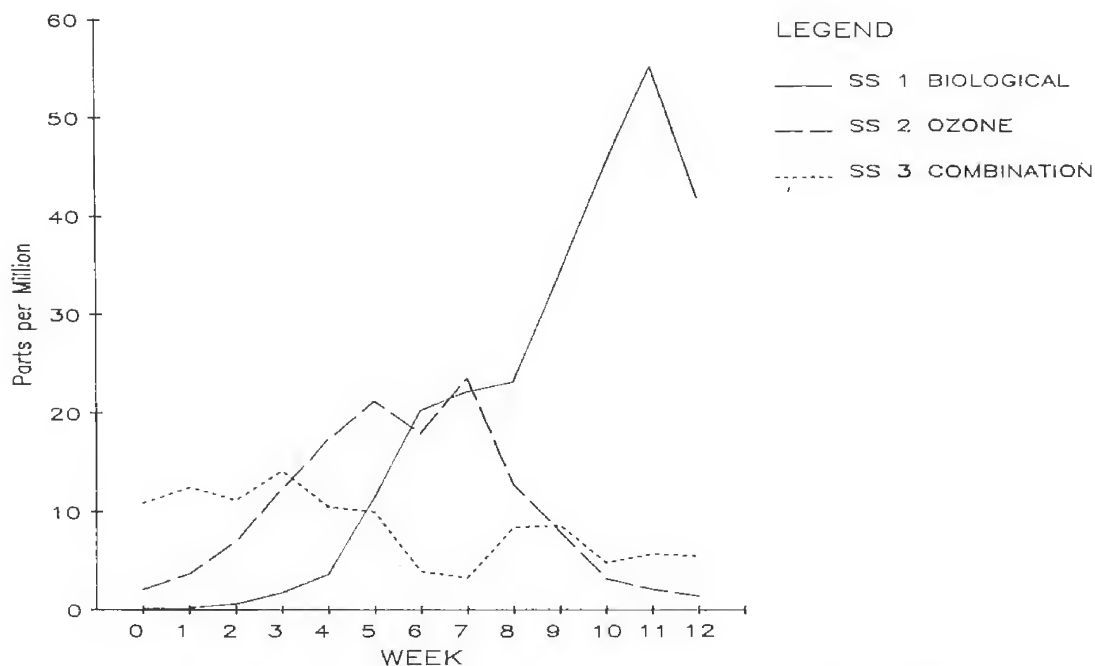


Figure 8. Graph of nitrite monitored over a 12-week period for three shrimp systems.

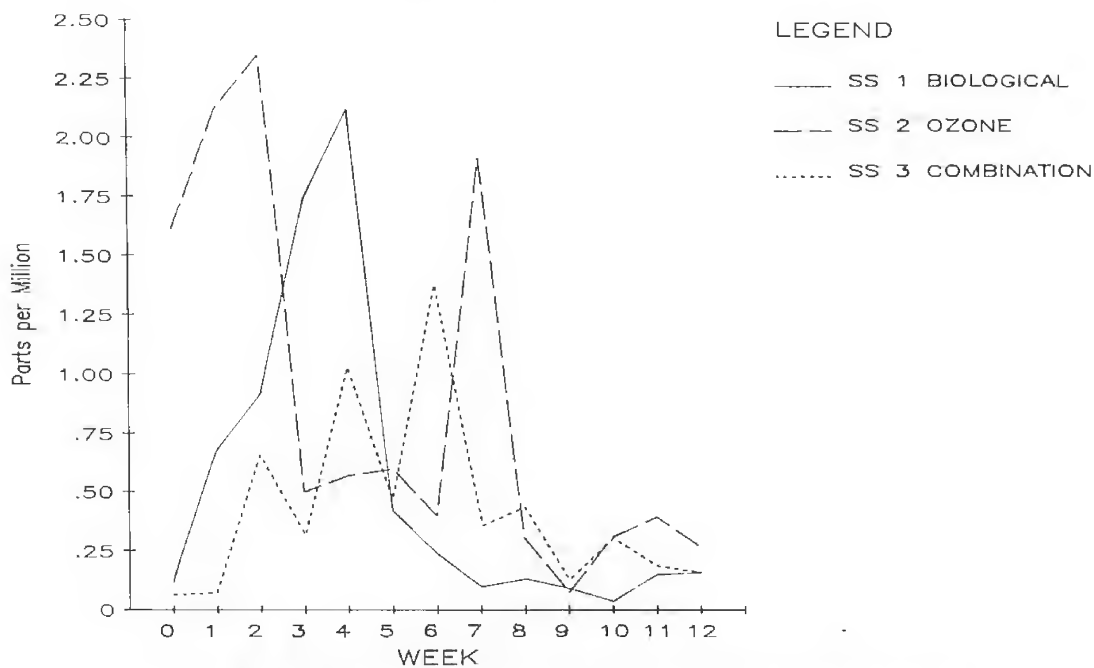


Figure 9. Graph of nitrate monitored over a 12-week period for three shrimp systems.

concentration, while the skimmer for SS-3a and 3b reduced the ammonia level. Ammonia was removed by the venturi in SS-2a and by the filter in SS-3a (Table 2). Nitrate was removed at a rate of 0.26 to 0.81 ppm from all systems except SS-2a. Most removal of nitrate from the systems occurred in the lamellar separator (Table 3).

The heterotrophic bacterial levels remained about the same throughout the study for both SS-1 and SS-2a (Fig. 10). Levels were basically the same for the two systems until week 11, when SS-1 was cleaned and a 80% water change was made. Although the bacterial level increased in SS-2a for this week, SS-1 levels decreased below the initial level. Numbers of presumptive *Vibrio* spp. decreased slightly for both systems through week 4 and increased through week 11. In all but one sample, (week 4), counts for the ozonated system were higher than for the biological system (Fig. 11). During two of the weeks, counts were considerably higher than initial levels.

#### DISCUSSION

Growth of *P. vannamei* in the closed systems was consistent with rates recorded for the species in various systems. Under experimental conditions, growth as high as

3 g/wk have been reported (Ogle 1992). At higher stocking densities, Reid (1989) reported growth of 0.57 and 0.61 g/wk (Table 4). Under commercial pond production with high flushing rates, *P. vannamei* growth rates of 0.27 to 1.85 g/wk have been recorded (Table 5). However, the target production period of 12 weeks resulted in 9 to 13 g animals. In order to achieve three crops per year, 1.8 g/wk growth will be necessary for reliable production of a 20 g animal in a 12-week growout period.

Survival rates were disappointing. Commercial ponds expect an 80-95% survival rate to make production feasible. In SS-1, SS-2a and SS-3a, numerous shrimp were lost when they jumped out of the culture tanks and escaped into other parts of the system.

Bacterial levels were expected to be minimal in SS-2a with ozone treatment. Actually, heterotrophic bacteria counts were higher in SS-2a than in SS-1 for most of the 12-week period. Apparently, ozone was being consumed in the system by the high solid organic content. Before repeating this study, modifications should be made to remove solids from the system.

Some biological filtration and denitrification was occurring in the lamellar. The nitrification occurring in the pump was unexpected and suggests that oxidation may have taken place due to air entrapment.

TABLE 2

Percent change in total ammonia between inflow and outflow of different filter components for four closed systems.

| System                    | 2a     | 2b     | 3a    | 3b     |
|---------------------------|--------|--------|-------|--------|
| Pump                      | -13.5  | -8.9   | -15.5 | -3.2   |
| Lamellar                  | -8.5   | -2.2   | +3.2  | -6.3   |
| Cyclone                   |        |        |       | -1.5   |
| Skimmer (O <sub>3</sub> ) | +19.7  | +4.1   | -4.0  | -7.0   |
| Filter                    |        |        | -17.7 | -12.2  |
| Venturi (O <sub>3</sub> ) | -25.2  | -12.8  |       |        |
| Reservoir                 |        |        | -26.8 |        |
| Total ppm                 | -0.043 | -0.050 | -0.30 | -0.047 |

All numbers based on an average of three samples.

TABLE 3

Percent change in nitrate levels between the inflow and outflow of different filter components for four closed systems.

| System                    | 2a    | 2b    | 3a    | 3b    |
|---------------------------|-------|-------|-------|-------|
| Pump                      | -15.7 | +0.2  | +2.7  | -0.6  |
| Lamellar                  | +9.5  | -2.8  | -23.7 | -19.8 |
| Hydrocyclone              |       |       |       | -1.0  |
| Skimmer (O <sub>3</sub> ) | +3.4  | +1.7  | +1.9  | -3.9  |
| Filter                    |       |       | -2.0  | +1.0  |
| Venturi (O <sub>3</sub> ) | +19.4 | 0.0   |       |       |
| Reservoir                 |       |       | +15.4 |       |
| Total ppm                 | +1.28 | -0.26 | -0.37 | 0.81  |

All numbers based on average of three samples.

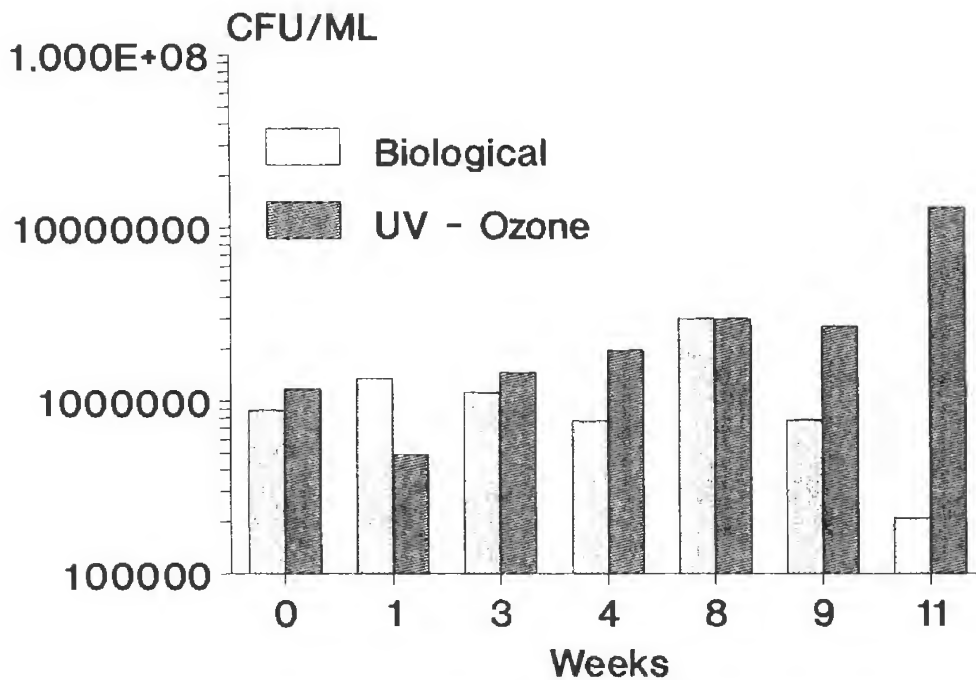


Figure 10. Total heterotrophic bacteria determined weekly for SS-1 and SS-2a.

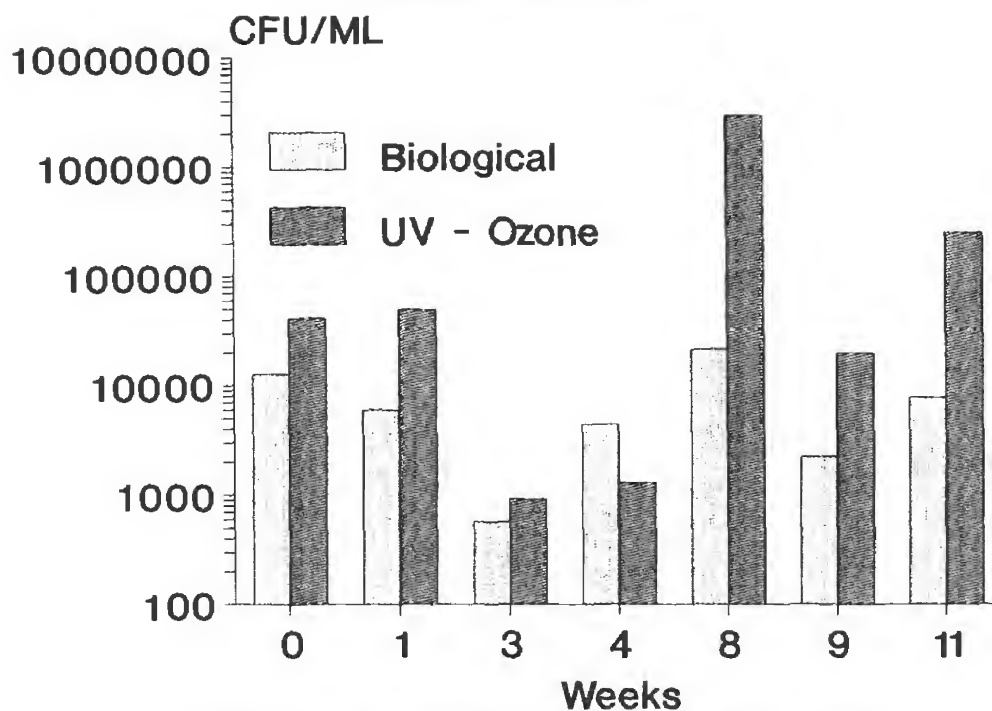
Figure 11. Presumptive *Vibrio* spp. sampled weekly for SS-1 and SS-2a.

TABLE 4  
Closed system growth (g/wk) of penaeid shrimp

| Species                | Minimum | Maximum | References                 |
|------------------------|---------|---------|----------------------------|
| <i>P. aztecus</i>      | 0.34    | 0.55    | Forster and Beard 1974     |
|                        | 0.20    | 0.53    | Mock, Ross and Salser 1977 |
| <i>P. indicus</i>      | 0.60    | 0.83    | Forster and Beard 1974     |
| <i>P. japonicus</i>    | 0.55    | 0.80    | Forster and Beard 1974     |
| <i>P. merguensis</i>   | 0.33    | 0.55    | Beard, et al. 1977         |
| <i>P. monodon</i>      | 0.80    | 1.58    | Forster and Beard 1974     |
| <i>P. occidentalis</i> | 0.57    | 0.78    | Forster and Beard 1974     |
| <i>P. orientalis</i>   | 0.91    | 1.42    | Forster and Beard 1974     |
| <i>P. setiferus</i>    | 0.32    | 0.42    | Forster and Beard 1974     |
|                        | 0.25    | 0.52    | Mock, Neal and Salser 1973 |
| <i>P. stylirostris</i> | 0.12    | 0.39    | Kennedy 1980               |
| <i>P. vannamei</i>     | 0.57    | 0.61    | Reid 1989                  |
|                        | 0.59    | 0.99    | Ogle 1992                  |

**TABLE 5**  
**Growth of *Penaeus vannamei* at various densities.**

|                         | System<br>Size      | System<br>Type | Density<br>#/m <sup>2</sup> | Growth<br>g/wk |
|-------------------------|---------------------|----------------|-----------------------------|----------------|
| Wyban and Sweeney 1990  | 330 m <sup>2</sup>  | pond           | 45                          | 1.4            |
|                         |                     |                | 75                          | 1.75           |
|                         |                     |                | 100                         | 1.4            |
|                         |                     |                | 150                         | 1.07           |
| Aquacop 1989            | 1000 m <sup>2</sup> | pond           | 139                         | 0.60, 0.72     |
| Reid 1989               | —                   | closed         | 970                         | 0.57           |
|                         |                     |                | 1539                        | 0.61           |
| Ogle (unpublished data) | 100 m <sup>2</sup>  | pond           | 100                         | 0.38           |
|                         |                     |                | 16                          | 0.80           |
|                         |                     |                | 1                           | 1.85           |
| Ogle 1992               | 1.8 m <sup>2</sup>  | tank           | 6.5                         | 3.29           |
|                         |                     |                | 13.7                        | 2.31           |
|                         |                     |                | 27.3                        | 1.40           |
| This report             |                     | closed         | 200                         | 0.87, 0.99     |
|                         |                     |                | 367                         | 0.59           |
| Sandifer, et al. 1987   | 28 m <sup>2</sup>   | tank           | 10                          | 1.41*          |
|                         |                     |                | 20                          | 1.35*          |
|                         |                     |                | 40                          | 1.11*          |
| Sandifer, et al. 1988   | 0.25 ha             | pond           | 12                          | 0.94*          |
|                         |                     |                | 42.5                        | 0.84*          |
|                         |                     |                | 20                          | 0.56**         |
|                         |                     |                | 40                          | 0.52**         |
|                         |                     |                | 60                          | 0.51**         |
|                         |                     |                | 100                         | 0.57**         |
| Trimble, W. 1980        | 0.08 ha             | pond           | 2.5                         | 1.8            |

\*calculated, \*\*estimated for 166-day growout

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## EFFECTS OF SALINITY ON SURVIVAL AND GROWTH OF POSTLARVAL *PENAEUS VANNAMEI*

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**ABSTRACT** Eight and 22-day-old *Penaeus vannamei* postlarvae were exposed to several salinities for 24 hours and 120 hours by direct transfer from 32 ppt salinity to lower salinity waters. The challenge study included six experiments conducted on 8-day-old postlarvae (PL-8) and five experiments conducted on 22-day-old postlarvae (PL-22). Each experiment consisted of ten replicates of ten animals each. Shrimp were held in 1 L plastic containers with 500-ml of seawater. Lowered salinity resulted in lower survival for shrimp of both ages. Longer exposure time resulted in lower survival for shrimp of both ages. Younger shrimp exhibited lower survival than older shrimp. Survival of 8-day-old postlarvae after 24-hour exposure to salinities of 32, 16, 8, 4, and 2 ppt was 97.3%, 92.8%, 19.8%, 8.2% and 1.7%, respectively. Survival of 22-day-old postlarvae after 24-hour exposure was 99.2%, 97.8%, 83.8%, 63.4% and 40.2%, respectively. A second series of experiments investigated the effect of salinity upon growth of 22-day-old postlarvae which had been acclimated to four different salinities (16, 8, 4, and 2 ppt). Thirty shrimp were stocked in triplicate into 113 L (30 gal) aquaria and fed a prepared commercial feed. Growth was determined after 30 days at 16°C and 28-30°C. Growth was greatest at higher temperatures, but statistically significant differences due to salinity were not detectable. Nonetheless, best observed growth occurred at the intermediate salinities of 8 and 4 ppt.

### INTRODUCTION

Shrimp of the genus *Penaeus* encounter a wide variety of salinities throughout their life cycle. Most penaeid species mature and reproduce in high salinity open ocean waters. Subsequently, the larvae migrate into lower salinity estuarine nursery areas where they metamorphose into postlarvae and grow rapidly (Gunter *et al.* 1964). Juveniles of *Penaeus aztecus* have been captured in Gulf of Mexico waters of 0.80 ppt salinity, and juveniles of *P. fluvialis* (= *P. setiferus*) have been found in salinities as low as 0.42 ppt (Gunter and Shell 1958). At the other extreme, juvenile *P. setiferus* have been captured in water with salinities as high as 43.3 ppt (Gunter 1961) and *P. brasiliensis* have been captured in waters ranging from 40-60 ppt (Chung 1980).

Although young shrimp tolerate a wide variety of salinities, they may show preferences for salinities within narrower ranges. For example, Chung (1980) found that 80% of the postlarval *P. brasiliensis* which he tested preferred salinities from 5-28 ppt, even though the animals had been captured in a high salinity (40-60 ppt) lagoon. On the other hand, Zein-Eldin (1963) demonstrated that wild-caught *P. aztecus*, *P. duorarum*, and *P. setiferus* postlarvae all had high survival rates and exhibited no differences in growth rate in salinities ranging from 2 to 40 ppt. This led Zein-Eldin to surmise that salinity may be of less importance than other factors in postlarval development.

*Penaeus vannamei*, the most popular aquacultured shrimp in the Western Hemisphere, has been reported to

have the greatest tolerance for low salinity water (1-8 ppt) of four penaeids from west Mexico (Mair 1980). In Ecuador, wild-caught *P. vannamei* postlarvae have been reported to grow in ponds with salinities below 2 ppt by Chauvin (1983) and in 0 ppt salinity by Garston (1986). Wulff (1987) reported culturing this species in Arizona utilizing total freshwater. In laboratory experiments, Olin and Fast (1987) determined that transfer of 5 to 12-day-old postlarval *P. vannamei* from 32 ppt salinity water directly into water of 20 or 36 ppt salinity resulted in survivals of 89% and 99%, respectively.

The only experimental data for *P. vannamei* growth in low salinities is that of Huang (1983). He measured the growth of postlarval *P. vannamei* after 30 days in waters of 5, 15, 25, 35, and 45 ppt and found that fastest growth occurred at 25 ppt, while poorest growth occurred at 45 ppt.

Studies on the survival and growth of postlarval *P. vannamei* in low salinity water are valuable to shrimp farmers along the Northern Gulf of Mexico. Coastal salinities may be as low as 2 ppt in the spring (Ogle 1989), when postlarvae are generally stocked into ponds. Further, shrimp in ponds are often subjected to rapid salinity drops after rainfall.

In this paper, we report the results of investigations concerning the effect of rapid salinity decreases on the survival of postlarval *P. vannamei*. We also attempt to determine the effect of low salinity on growth of *P. vannamei* after a period of acclimation to low salinity.

## MATERIALS AND METHODS

All studies were conducted using artificial sea salts (Instant Ocean) dissolved in tap water. For each experiment, waters of various salinities were prepared from a common stock of seawater with a salinity of 32 ppt. At least three days prior to each experiment, the stock seawater was diluted with fresh tap water to achieve salinities of 16, 8, 4, and 2 ppt. Higher salinities (32 and 16 ppt) were measured with a refractometer, while lower salinities (8, 4 and 2 ppt) were measured with a hydrometer. During each experiment, continuous illumination was provided by six 40-watt fluorescent bulbs.

Five-day-old postlarval shrimp were obtained from two Florida-based commercial hatcheries. Shrimp arrived at 16–18°C in 32–34 ppt seawater. Postlarvae from each shipment were held for three days in 32 ppt seawater and fed brine shrimp nauplii (*Artemia* sp.) three times daily, *ad libitum*, before beginning experiments. Each shipment of shrimp was divided into three groups, one for each of three studies.

## SALINITY SHOCK

*Study 1: 8-day-old postlarvae*

The first group of shrimp from each shipment was challenged when they were 8 days old by direct transfer into waters of one of five salinities (32, 16, 8, 4, or 2 ppt). White 1 L plastic bowls containing 500 ml of seawater were used as experimental chambers. Ten chambers for each salinity (32, 16, 8, 4, and 2 ppt) were utilized. Each chamber was stocked with ten postlarvae. Two hours were required to transfer the postlarvae to the experimental chambers. Chambers were loosely fitted with lids to reduce evaporation. Temperatures were maintained by placing chambers in a constant-temperature water bath.

Experiments were conducted on six separate shipments of 8-day-old postlarvae. Animals were fed live *Artemia* sp. nauplii and freeze-dried calanoid copepods (Kordon microplankton) immediately after being stocked and three times daily thereafter. Dead shrimp were removed daily. Survival of animals in each chamber was recorded at 24 hours and 120 hours.

*Study 2: 22-day-old postlarvae*

The second group of animals from each shipment was held in water of 32 ppt salinity until they were 22-days-old. The shrimp were then challenged by direct transfer to waters with salinities of 32, 16, 8, 4, and 2 ppt. All procedures employed in Study 1 were followed for the five experiments conducted on 22-day-old postlarvae.

## SALINITY ACCLIMATION

*Study 3: Survival and growth of 22-day-old post-larvae acclimated to lower salinities*

The third group of postlarval shrimp was gradually acclimated to the various salinities prior to the start of the experiments. Shrimp were divided among four 113 L aquaria and acclimated separately to the lower salinities of 16, 8, 4, and 2 ppt. Salinity in each aquarium was lowered at a rate of 2 ppt per day by adding aged tap water. The acclimation regime achieved the desired salinities by the time that the experiment was initiated (Day 0). Acclimation of shrimp to 2 ppt began 14 days prior to stocking, to 16 ppt began seven days before stocking and so on. During the acclimation period, shrimp were gradually weaned from a diet of *Artemia* sp. nauplii and copepods to a Rangen-Zeigler postlarval feed.

These experiments were performed in triplicate in all-glass aquaria containing 113 L of seawater. Each aquarium was stocked with 30 postlarvae. Shrimp were individually weighed to the nearest 0.01 g on an electronic balance. A subsample of 25 postlarvae from each of the salinities was weighed on Day 0 after the acclimation period and prior to the start of each experiment. When the experiments began, postlarvae were less than 0.01 g (wet weight). All surviving shrimp were weighed on Day 30. Total weight gain was used as an indicator of growth because Zein-Eldin (1963) and Raj and Raj (1982), working with postlarval penaeid shrimp, found that weight increased faster than length and was therefore a more sensitive indicator of growth.

Three separate experiments were conducted in this study. The first two experiments were run simultaneously using shrimp from the same shipment. In experiment 1, water temperatures were maintained at 30°C ± 3°C (high temp). In experiment 2, water temperatures were maintained at 16°C ± 2°C (low temp). The third experiment was run at a different time and utilized a different shipment of shrimp than the first two experiments. During experiment 3, water temperatures were maintained at 28°C ± 1°C. Temperatures were controlled by regulating the room temperature or by aquarium heaters. All three experiments were conducted at each of four salinities (16, 8, 4, and 2 ppt).

No substrate was used in the aquaria. Filtration was provided by an external power filter (Dynaflow 600). Previous experiments on 22-day-old postlarvae demonstrated that the postlarvae were too small to handle the currents and would be held against the filter screens during the first week. Death resulted when the shrimp were held against the screens for periods longer than an hour. To prevent loss of postlarvae, the intake pipe of the power filter was screened. Additionally, during the first week of growth the filters were run only an hour a day.

Salinities were checked twice weekly and maintained at the appropriate salinity levels by the addition of freshwater. Salinity fluctuations were less than 1 ppt. Addition of plexiglass lids reduced evaporation and prevented the shrimp from jumping out of the tanks.

#### DATA ANALYSIS

Survival data were analyzed as percent survival using the Kruskal-Wallis nonparametric analysis of variance. Pairwise comparisons were performed with the Mann-Whitney U-test using Bonferroni's criterion of significance. Differences were considered to be significant if  $P < 0.05$ .

Growth was determined as final wet weight of shrimp. The analysis of growth as a function of temperature and salinity was analyzed using a two-way nested analysis of variance where the replicated aquaria provided the error term for hypothesis testing. Differences were considered to be significant if  $P < 0.05$ .

### RESULTS

#### SALINITY SHOCK

##### *Effect of age at exposure on ability to survive a salinity drop*

Figure 1 displays the survival of 8-day-old postlarvae (PL-8) and 22-day-old postlarvae (PL-22) of *P. vannamei* at 24 hours and 120 hours after challenge to various lowered salinities. The Kruskal-Wallis test detected significant differences in overall survival (combined 24 hours and 120 hours) between PL-8 and PL-22. Mann-Whitney U-tests at each salinity revealed that overall survival (combined 24 hours and 120 hours) was significantly lower for eight-day-old postlarvae than for 22-day-old postlarvae at 16, 8, 4, and 2 ppt salinity. No differences in survival due to age were detected at the initial salinity of 32 ppt.

##### *Effect of salinity challenge on survival of 8-day-old postlarvae*

Survival of 8-day-old postlarvae after 24 hours exposure to salinities of 32, 16, 8, 4, and 2 ppt was 97.3%, 92.8%, 19.8%, 8.2%, and 1.7%, respectively. The Kruskal-Wallis test detected significant differences in overall survival due to salinity. There was no significant difference (Mann-Whitney U-test) in survival percentage between PL-8s transferred to 32 ppt (control) and those transferred to 16 ppt (Figure 2). There was no significant difference in survival between PL-8s exposed to 4 and 2 ppt. Survival was significantly higher for PL-8s transferred to 8 ppt than those transferred to lower salinities. There was a significant reduction in survival between animals exposed to 16

ppt and those exposed to 8 ppt. This trend was obvious in both the 24-hour and 120-hour experiments.

Figure 2 reveals that although the observed survival rates were lower at 120 hours than at 24 hours, the differences were statistically significant by the Mann-Whitney U-test only at the higher salinities (32 ppt and 16 ppt).

##### *Effect of salinity challenge on survival of 22-day-old postlarvae*

Survival of 22-day-old postlarvae after 24 hours exposure to 32, 16, 8, 4, and 2 ppt was 99.2%, 97.8%, 83.8%, 63.4%, and 40.2%, respectively. Figure 3 exhibits the effect of salinity challenge on 22-day-old postlarval survival. The Kruskal-Wallis test detected significant differences in overall survival due to salinity. Significantly lower survival was detected for animals transferred from 32 ppt to 4 and 2 ppt salinity (Mann-Whitney U-test). Survival of animals exposed to 4 ppt was lower than survival of animals exposed to 8 ppt. Survival was also lower for animals exposed to 8 ppt than for animals exposed to 16 ppt. There was no significant difference in survival percentage between PL-22s transferred to 32 ppt (control) and those transferred to 16 ppt.

Survival of postlarvae after 24 hours exposure was generally higher at all salinities than after 120 hours exposure. Statistically significant differences for time of exposure are also indicated on Figure 3.

#### SALINITY ACCLIMATION

##### *Effect of acclimation to lowered salinity on survival of 22-day-old postlarvae*

Figure 4 compares the survival of shrimp acclimated to lower salinities at two temperatures. The Kruskal-Wallis test failed to detect differences in survival due to salinity at a temperature of 16°C. However, differences were detected at the higher temperatures where shrimp displayed a greater sensitivity to salinity (Mann-Whitney U-tests detected lower survival at 2 ppt than at 16 ppt).

##### *Effect of salinity acclimation and temperature on growth rate*

Postlarval *P. vannamei* grew fastest at higher temperatures (Figure 5). The two-way nested analysis of variance detected greater final weights for shrimp reared at 30°C than those at 16°C. Animals maintained at 28-30°C were nearly twice as large as those grown at 16°C.

There were no statistically detectable differences in growth among shrimp maintained at the four salinities. However, the greatest final weights were attained in the intermediate salinities (8 and 4 ppt) at both temperatures.

Interestingly, there were large differences between shipments of shrimp in overall performance. Animals in experiment 2 (30°C) reached 1 g in both 8 ppt and 4 ppt

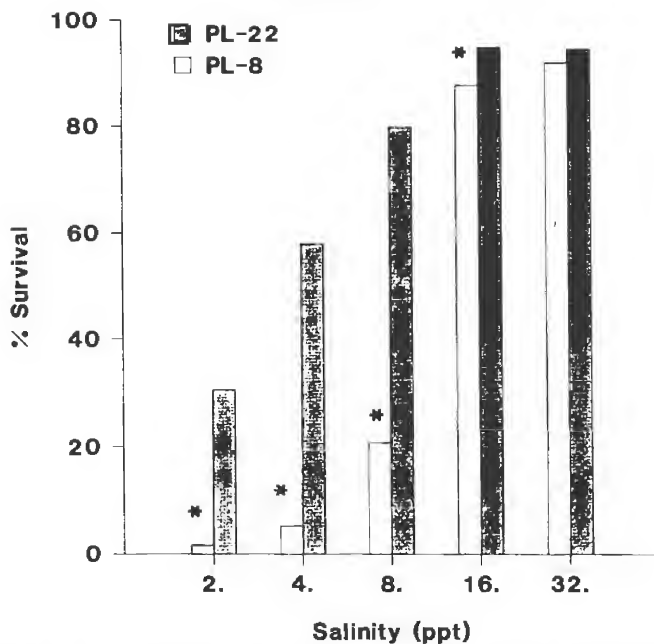


Figure 1. Survival of salinity shock by 8-day-old and 22-day-old postlarval *Penaeus vannamei*. Asterisks denote statistically significant differences in survival between shrimp of the two ages.

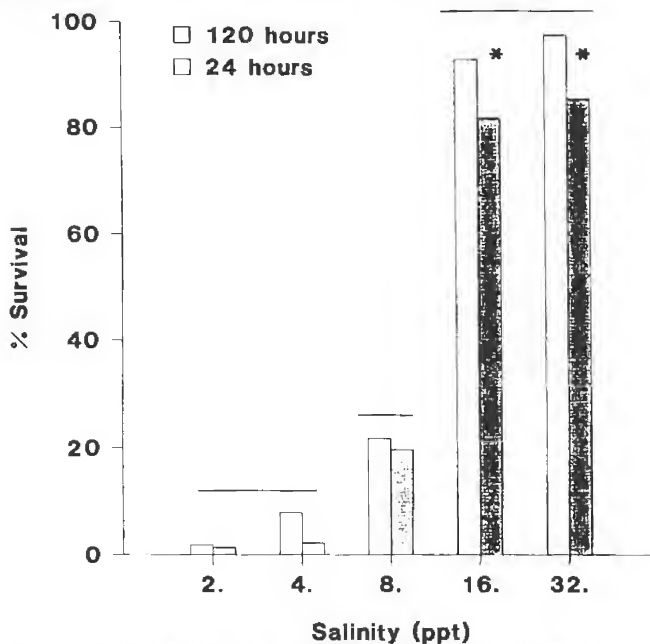


Figure 2. Survival of salinity shock by 8-day-old postlarval *Penaeus vannamei* for 24 and 120 hour exposures. Salinities sharing a line are not statistically different from one another. Asterisks denote statistically significant differences in survival between shrimp exposed for 24 hours or 120 hours at each salinity.

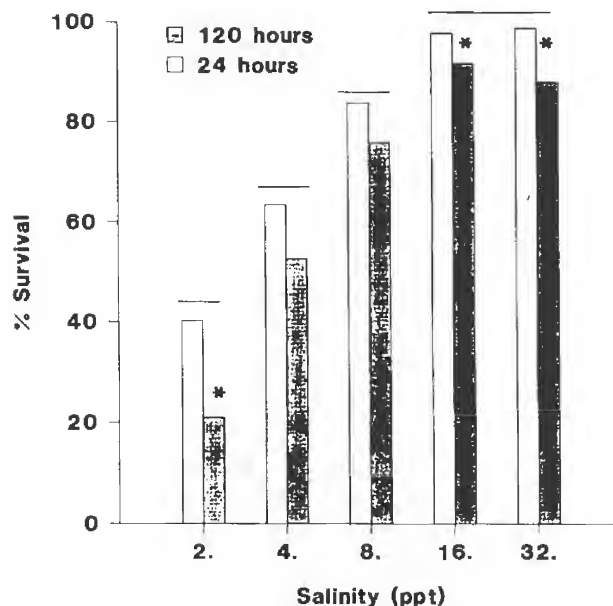


Figure 3. Survival of salinity shock by 22-day-old postlarval *Penaeus vannamei* for 24 hour and 120 hour exposures. Salinities sharing a line are not statistically different from one another. Asterisks denote statistically significant differences in survival between shrimp exposed for 24 hours or 120 hours at each salinity.

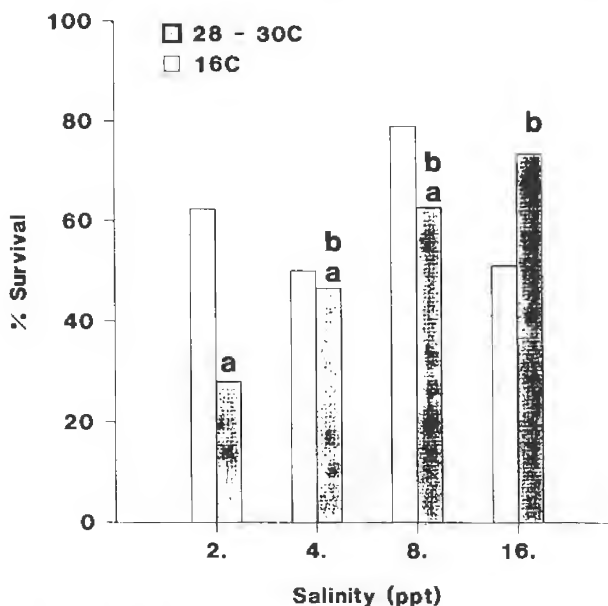


Figure 4. Effects of temperature on survival of 22-day-old postlarval *Penaeus vannamei* acclimated to low salinity. There are no statistically significant differences among salinities for shrimp maintained at 16°C. For shrimp maintained at 28°C and 30°C, salinities sharing a letter are not statistically different from each other.

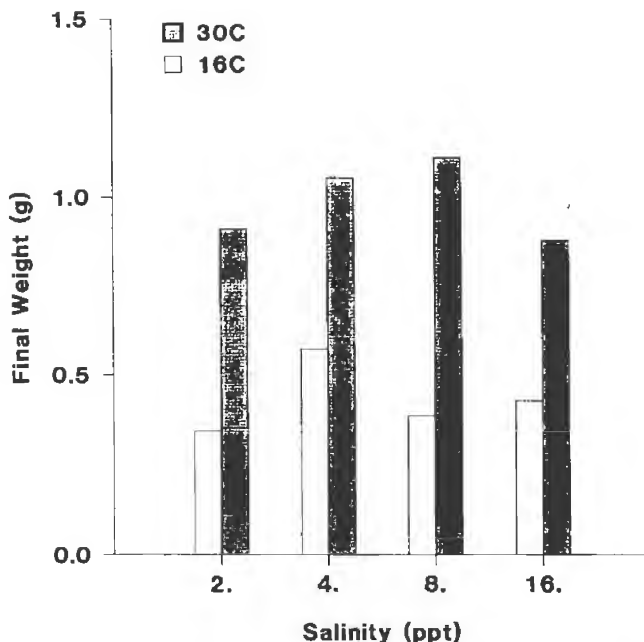


Figure 5. Final weights of *Penaeus vannamei* grown for 30 days at two temperatures. There is a statistically significant difference between the temperatures, but there are no significant differences due to salinity at either temperature.

seawater. Animals grown in both 16 ppt and 2 ppt seawater at 30°C failed to attain a size of 1 g. Animals from a different shipment of shrimp grown at 28°C demonstrated negligible growth at any salinity and therefore were excluded from the growth rate analysis.

#### DISCUSSION

Our results on the tolerance of postlarval *P. vannamei* to rapidly-lowered salinities are consistent with other studies of penaeids. Zein-Eldin and Aldrich (1965) report lower survival of *P. aztecus* when exposed to reduced salinities for more than 24 hours. Biesiot (1975) noted that 22-day-old *P. aztecus* were more tolerant to challenge by low salinity than 10-day-old postlarvae. In studies on four penaeid species, Mair (1980) found that as shrimp became older and increased in size, their salinity preferences altered and they were apparently able to adjust more readily to lower salinities.

In our studies, postlarvae of *P. vannamei* had greater observed survival at 24 hours than at 120 hours. The differences in survival at a particular age which we noted between 24 hours and 120 hours are due to time of expo-

sure. The survival rate (deaths per hour) is no different at 24 hours than at 120 hours, even though the total number of deaths was greater at 120 hours for each salinity and age.

There was a great deal of variability in survival among the different shipments of postlarvae tested. Ability of postlarvae to withstand stresses is known to vary considerably and is apparently correlated with overall performance in aquaculture settings. In fact, postlarvae collected from full seawater in the wild in Ecuador which are destined for shrimp culture ponds are subjected to a three-minute brackish water stress test bath (15 ppt) to assess their vigor (Maugle, personal communication). A simple salinity stress test was used by Tackaert et al. (1989) to evaluate nutritional differences for three species of penaeids including *P. vannamei*.

Although we were unable to detect statistically significant differences in growth rate attributable to salinity, the greatest observed growth rates occurred at 8 and 4 ppt salinities. In a commercial setting, *P. vannamei* stocked into nursery ponds are expected to achieve a size of 1 g in 30 to 50 days (Shleser and Follett 1984). The growth of shrimp at 30°C in this study was acceptable by this criterion at salinities of 8 and 4 ppt. Growth at 16°C was below this criterion at all salinities. Zein-Eldin and Griffith (1969)

have shown that *P. aztecus* and *P. setiferus* postlarvae were adversely affected by low salinities when held at low temperatures. Sturmer and Lawrence (1989) found that a combination of high salinity and high temperature had an adverse effect on production of *P. vannamei* postlarvae.

As with survival, growth of *P. vannamei* under laboratory conditions is highly variable and often unpredictable (Ogle 1992). The lack of growth in the group of shrimp held at 28°C was probably not due to temperature, but indicative of the variability of the animals. Olin and Fast (1989) tested *P. vannamei* and *P. monodon* postlarvae in acclimation studies. When different groups of postlarvae were tested under the same conditions, there appeared to be significant differences in growth among the groups. This points out the critical need for using as many replicates as possible when designing and performing experiments on shrimp growth and survival.

Even though greatest growth was found in waters with salinities of 8 and 4 ppt, percentage survival was better at 16 ppt. We feel that postlarval shrimp would have a higher survival rate if stocked into lower salinity ponds (between 16 and 8 ppt) as PL-22s rather than PL-8s. We do not know if the additional cost of holding the shrimp for the added 12 days would offset the cost of additional postlarvae.

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# VARIABILITY IN GROWTH OF POSTLARVAL *PENAEUS VANNAMEI*

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**ABSTRACT** This note reports the average size of *Penaeus vannamei* postlarvae held under a variety of conditions for approximately 30 days. Fifteen separate and independent rearing trials were completed over several seasons. Extreme growth variations were noted, with significant differences existing in eight of the 26 replicates. Significant differences were noted for treatments in seven of the 12 studies. Shrimp ranged in size from an average of 0.01 to 3.08 g after a month of culture.

## INTRODUCTION

Commercial aquaculture in the Americas typically involves culture of the South American white legged shrimp, *Penaeus vannamei*, in earthen or plastic-lined nursery ponds (Sturmer and Lawrence 1987). Postlarvae stocked into nursery ponds are expected to achieve a 1 g size in 30 to 45 days. After this nursery period, the juveniles are stocked into large earthen growout ponds.

The use of nursery ponds increases the feed efficiency for the postlarvae and provides better inventory control for the stocking of production ponds. Extending the growing season is one advantage of using nursery ponds in the United States. During the colder months, shrimp culture may be started indoors under controlled conditions. At the Gulf Coast Research Laboratory (GCRL), rearing trials of postlarval *P. vannamei* were conducted under a variety of conditions. Results of those independent trials are presented here.

## MATERIALS AND METHODS

*P. vannamei* postlarvae obtained from a number of commercial and research hatcheries in the United States and abroad were reared at GCRL. Most studies utilized 113 L, all-glass aquaria stocked with 30 animals each (108/m<sup>2</sup>). Several 1.5 m diameter by 1.5 m deep kalwall tanks (Solar Components Corp., Manchester, New Hampshire), rectangular tanks (0.96 m x 1.9 m x 0.3 m) 1.84m<sup>2</sup> and a pond (683 m<sup>2</sup>) were also used in some of the studies as noted. Shrimp were stocked at densities ranging from 100/m<sup>2</sup> to 4,000/m<sup>2</sup>.

Outside studies utilized aquaria or tanks exposed to full sunlight. Tanks placed under a roofed porch received indirect sunlight. With the exception of one location study in a shed, aquaria maintained indoors were routinely kept at 28°C under constant light supplied by six 40-watt fluorescent bulbs. One study used additional 30-watt lighting directly over each aquaria and *Fucus* sp. algae. Another

study used 15-watt lighting over each aquaria and *Gracilaria* sp. algae. Illumination provided by six seven-watt bulbs of three colors (red, green and blue) and a combination of the three colors were utilized in one study. The aquaria were wrapped in black plastic to shield them from incidental light. A study on substrates used five plastic screens suspended longitudinally in each of three tanks, while *Gracillaria* sp. algae was used as the substrate in three additional tanks. A production trial was conducted in a pond containing floating round cages constructed of 500 micron plastic screen with a volume of 1 m<sup>3</sup>. A final study utilized three aquaria outside and three aquaria inside plumbed into a common water source. The aquaria were placed in water baths which also shared a common water source. Three additional aquaria indoors were not plumbed into the common water system, but shared the indoor water bath.

Aeration was provided by a single airstone to all treatments with the exception of the pond. A prepared commercial postlarval diet (Zeigler Bros, Inc., Gardners, Pennsylvania) was used in all treatments and shrimp were fed *ad libitum*. All studies utilized water of 16 ppt salinity. Artificial seawater prepared from aged tap water and a commercial sea salt was used in all aquarium studies. Natural sunlight and natural bay water were used in the kalwall tank and pond studies. The postlarvae (PLs), 10 to 36 days old, weighed several milligrams at the time of stocking. After the growth period, all shrimp were harvested, counted and individually weighed to the nearest milligram on an electronic balance. Numbers were averaged and a standard deviation calculated. Significance ( $\alpha = 0.01$ ) between replicates and between treatments for each study were calculated using analysis of variance (ANOVA). Shrimp growth was expected to increase fourfold after one month. Therefore, growth was not determined in percent increase but reported as final wet weight.

General categories of variability included production, polyculture, light, algae, substrate, source of PLs, feeding rate, water depth and indoor versus outdoor locations.

## RESULTS

Growth was extremely variable, resulting in a final average size after 30 days from 0.01 g to 3.08 g (Table 1). Significant differences existed in eight of 26 replicates and seven of 12 treatments. Production trials resulted in sizes of 0.37 (Study A) and 0.10 g (Study N). A feeding trial resulted in a final size of 0.07 and 0.09 g (Study D). Polyculture resulted in sizes of 1.32 (Study E) and 0.28 g (Study F). The use of various colored lights resulted in sizes of 0.04 and 0.05 (Study I). It was interesting to note that the shrimp held under green light turned a deep blue color. The use of a macroalgae substrate and additional light resulted in sizes of 0.14 (Study K) and 0.72 g (Study L). The use of substrate screens resulted in a size of 0.29 g (Study M). Animals obtained from different sources achieved sizes ranging from 0.01 (Study G) to 1.16 g (Study H). The growth at three water depths ranged from 1.02 in the 5 ft depth to 1.34 g in the 3 ft depth (Study B). A comparison of inside with outside growth resulted in an outdoor size of 1.18 g (Study C) and 0.48 g (Study F). Final sizes of shrimp from inside static, inside flowing and outside flowing tanks were 0.81, 0.98 and 1.13 g (Study O). Best growth was recorded for animals held in the 683 m<sup>2</sup> pond (Study J). Shrimp held in cages in the pond reached a size of 1.20 when fed and 1.24 g when unfed. Animals stocked directly into the pond grew to a final size of 3.08 g (Study J). Shrimp in four of the 21 inside treatments (19%) achieved a size of 1 g, while shrimp in eight of the 11 outside treatments (73%) achieved 1 g in size. The maximum size achieved by shrimp in the four treatments held under the roofed porch was 0.47 g.

In the kalwell study (Study B), temperature ranges were similar in the 5 ft (80-96 F) and 3 ft (81-96 F) depth, but fluctuated more in the 1 ft (78-98 F) depth. In the study which compared location (Study C), water temperatures ranged from 73-100, 75-85 and 70-86 F for tanks located outside, under a porch and inside a shed, respectively. In the final study (Study O), the inside flowing and outside flowing aquaria generally maintained the same temperatures, whereas the inside static aquaria generally ranged 2 to 9 degrees lower.

## DISCUSSION

The animals placed in natural pond water showed remarkable growth. Leber and Pruder (1988) demonstrated a growth factor present in high density culture systems that promotes growth greater than 1.5 g/wk in production ponds. They showed that this water, when pumped indoors, still induced good shrimp growth. It should be noted that when animals from Study B were harvested and restocked into

the kalwell tanks, they also showed remarkable growth, increasing in size by 3.29 g during an 11-day period.

Direct statistical comparisons between trials were not possible due to differences in initial age, tank type, light source, seawater type and temperature. However, empirical comparisons are discussed. For all factors, examples can be found for both good and poor growth.

Shrimp growth is highly variable among groups of animals (Olin and Fast 1989), and even within the same group of animals. While this has been demonstrated by the significant differences reported in eight of the replicates with identical conditions, this is not always the case. Animals from four different sources (two different sources for each study) cultured under the same conditions within the same study achieved poor growth in Study G (0.01 g) and good growth in Study H (1.16, 1.14 g).

Animals cultured outside generally grow better than animals grown inside. Eight of the 11 outside treatments achieved a size greater than 1 g, while only four of the 21 inside treatments achieved a size greater than 1 g. This was contradicted in the polyculture Studies E and F. The shrimp cultured inside in Study E achieved a size greater than 1 g, while the shrimp cultured outside in Study F grew to a maximum size of 0.48 g. However, there was a significant difference in three of the four treatments in Studies E and F. All shrimp were held in aquaria without filtration at a density of 108 m<sup>2</sup> for 30 days. Although there was a difference in postlarvae age at the time of stocking, age does not appear to be the determining factor. The shrimp in Study H surpassed the 1 g size expected in a nursery system while the postlarvae in Study G showed negligible growth even though the animals were twice as old at the time of stocking (PL-12 vs PL-24, respectively). Also, the shrimp in Study H achieved the same size as the shrimp cultured without snails in Study E, even though Study E animals were three times as old (PL-36 vs PL-12). In all three studies, postlarvae were held inside in aquaria for 30 to 32 days at a density of 108 m<sup>2</sup>.

In these studies, all treatments that were located outdoors tended to be warmer than the 28°C temperature of indoor tanks. The shallower water depth used for the kalwell tanks also resulted in warmer temperatures. Aquaria placed outdoors tended to grow algae which may have conditioned the water or served as a supplemental feed source. The final study attempted to eliminate the influence of these factors by circulating both the culture water and the bath water. Temperatures and algae growth were the same for both the inside and outside flowing tanks, and no significant differences were noted for shrimp sizes. Significant differences in growth of shrimp in the inside replicates were noted. Therefore, the role of natural sunlight per se has not been demonstrated.

Table 1  
Nursery growth of *Penaeus vannamei* under a variety of conditions

| Study         | Location | Tank Type | Filter   | Density /m <sup>2</sup> | Age PL | Duration Days | Rep No. | Survival Percent | Stat | x Size g | SD    |
|---------------|----------|-----------|----------|-------------------------|--------|---------------|---------|------------------|------|----------|-------|
| A. production | outside  | kal       | none     | 274                     | 20     | 33-35         | 3*      | 39.7             |      | 0.37     | 0.126 |
| B. 5' depth   | outside  | kal       | none     | 108                     | 26     | 31            | 1       | 19.0             | a    | 1.02     | 0.338 |
| 3' depth      | outside  | kal       | none     | 108                     | 26     | 32            | 1       | 99.0             | b    | 1.34     | 0.335 |
| 1' depth      | outside  | kal       | none     | 108                     | 26     | 32            | 1       | 81.0             | a    | 1.14     | 0.395 |
| C. location   | outside  | tk        | none     | 100                     | 23     | 29-32         | 1       | 43.8             | a    | 1.18     | 0.389 |
|               | porch    | tk        | none     | 100                     | 23     | 35            | 1       | 69.2             | b    | 0.47     | 0.159 |
|               | inside   | tk        | none     | 100                     | 23     | 32            | 1       | 51.5             | c    | 0.65     | 0.248 |
| D. 1% feed    | inside   | aq        | dynafluo | 108                     | 14     | 32            | 3       | 68.3             | a    | 0.07     | 0.061 |
| 10% feed      | inside   | aq        | dynafluo | 108                     | 14     | 32            | 3       | 85.0             | a    | 0.09     | 0.073 |
| E. snails     | inside   | aq        | none     | 108                     | 36     | 32            | 3*      | 96.0             | a    | 1.32     | 0.357 |
| no snails     | inside   | aq        | none     | 108                     | 36     | 32            | 3       | 88.0             | b    | 1.16     | 0.380 |
| F. mullet     | outside  | aq        | none     | 108                     | 24     | 30            | 3*      | 93.3             | a    | 0.28     | 0.146 |
| no mullet     | outside  | aq        | none     | 108                     | 24     | 30            | 3*      | 98.9             | b    | 0.48     | 0.166 |
| G. source:    |          |           |          |                         |        |               |         |                  |      |          |       |
| Peruvian      | inside   | aq        | dynafluo | 108                     | 24     | 30            | 3       | 82.2             | a    | 0.01     | 0.019 |
| Guatemalan    | inside   | aq        | dynafluo | 108                     | 24     | 30            | 3       | 97.8             | a    | 0.01     | 0.006 |
| H. source:    |          |           |          |                         |        |               |         |                  |      |          |       |
| Oceanic Inst. | inside   | aq        | none     | 108                     | 12     | 30            | 2       | 88.0             | a    | 1.16     | 0.548 |
| GCRL          | inside   | aq        | none     | 108                     | 12     | 30            | 2       | 61.6             | a    | 1.14     | 0.540 |
| I. lights:    |          |           |          |                         |        |               |         |                  |      |          |       |
| green         | inside   | aq        | dynafluo | 108                     | --     | 30            | 3       | 67.0             | a    | 0.05     | 0.040 |
| red           | inside   | aq        | dynafluo | 108                     | --     | 30            | 3       | 76.0             | a    | 0.05     | 0.027 |
| blue          | inside   | aq        | dynafluo | 108                     | --     | 30            | 3       | 73.0             | a    | 0.04     | 0.021 |
| mixed         | inside   | aq        | dynafluo | 108                     | --     | 30            | 3       | 75.0             | a    | 0.05     | 0.033 |
| J. cage/fed   | outside  | pd        | none     | 108                     | 22     | 32            | 3*      | 73.3             | a    | 1.20     | 0.542 |
| cage/unfed    | outside  | pd        | none     | 108                     | 22     | 32            | 3       | 55.7             | a    | 1.24     | 1.173 |
| pond          | outside  | pd        | none     | ---                     | 22     | 32            | 1       | ---              | b    | 3.08     | 0.568 |
| K. bare       | inside   | aq        | none     | 108                     | --     | 30            | 1       | 7.0              | a    | 0.02     | 0.019 |
| with algae    | inside   | aq        | none     | 108                     | --     | 30            | 1       | 75.0             | a    | 0.06     | 0.045 |
| algae/light   | inside   | aq        | none     | 108                     | --     | 30            | 1       | 110.0            | b    | 0.14     | 0.067 |
| L. bare       | inside   | aq        | none     | 108                     | --     | 30            | 3       | 90.0             |      | 0.49     | SNA   |
| with light    | inside   | aq        | none     | 108                     | --     | 30            | 3       | 90.0             |      | 0.41     |       |
| algae/light   | inside   | aq        | none     | 108                     | --     | 30            | 3       | 90.0             |      | 0.72     | SNA   |
|               |          |           |          |                         |        |               |         |                  |      |          | SNA   |
| M. substrate: |          |           |          |                         |        |               |         |                  |      |          |       |
| screens       | porch    | tk        | none     | 1635                    | 10     | 37            | 3*      | 59.3             | a    | 0.29     | 0.170 |
| algae         | porch    | tk        | none     | 1635                    | 10     | 37            | 3       | 52.9             | a    | 0.35     | 0.218 |
| N. production | porch    | tk        | exchange | 4000                    | 10     | 30            | 2       | 58.0             |      | 0.10     | 0.033 |
| O. static     | inside   | aq        | none     | 108                     | 12     | 30            | 3*      | 107.0            | a    | 0.81     | 0.485 |
| flowing       | inside   | aq        | none     | 108                     | 12     | 30            | 3*      | 58.0             | ab   | 0.98     | 0.702 |
| flowing       | outside  | aq        | none     | 108                     | 12     | 30            | 3       | 22.2             | b    | 1.13     | 0.679 |

\* denotes replicates that are significantly different  
treatments sharing the same letter are not significantly different  
SNA — sample not analyzed

kal - Kalwell tank 1.8 m<sup>2</sup> = 5 foot diameter; aq - aquarium 0.279 m<sup>2</sup> = 3 gal; tk - tank 0.96-m x 1.9-m x 0.3 m; pond 683 m<sup>2</sup>  
inside - 24-h constant illumination; outside - full sunlight; porch - under cover with natural sunlight  
Study I used six seven-watt lights (red, green, blue and mixed) with aquaria wrapped in black plastic.  
Study J used *Fucus* sp. algae and 30-watt lighting

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The Effect of Salinity on Spawning Frequency of *Penaeus setiferus* in Aquaria

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## THE EFFECT OF SALINITY ON SPAWNING FREQUENCY OF *PENAEUS SETIFERUS* IN AQUARIA

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**ABSTRACT** *Penaeus setiferus* were matured and spawned in a small 120 L tank system in the absence of males. No significant differences in the number of shrimp that spawned or the time required to spawn were detected for shrimp held at salinities of 20, 25 or 30 ppt in either natural or artificial seawater. The earliest that spawning occurred was an average of 17 days past ablation and as late as 28 days past ablation. None of the shrimp held in artificial seawater at 20 and 25 ppt spawned in the same molt cycle in which they were ablated, while one third of the shrimp held in natural seawater did.

### INTRODUCTION

Interest in culture of marine shrimp has increased dramatically in the last decade. In 1980, 2% of the world's shrimp were farmed in ponds. In 1991, farmed shrimp provided 28% of the world's shrimp supply. The major limiting factor to further development is the hatchery production of postlarvae or seed (Rosenberry 1991). The production of seed by controlled sexual maturation of captive broodstock has been possible for marine shrimp since 1975. Experimental data on penaeid shrimp maturation and reproduction have been reviewed by Muthu and Laxminarayana (1982), Primavera (1985), Chamberlain (1985), Bray and Lawrence (1992), and Browdy (1992). Conditions representing the "industry standard" for maturation of *Penaeus vannamei* from commercial facilities have been documented by Ogle (1991a). It is the general recommendation of those reviews that clear, clean, ocean seawater of 28-32 ppt be utilized for maturation. Few sites can provide these conditions, compelling more than half of the maturation facilities to use some percentage of recirculation (Ogle 1991a). The salinity of the natural seawater available to the Gulf Coast Research Laboratory is generally much lower than the 28-32 ppt recommended for maturation. Therefore, the addition of artificial salts to the natural seawater is often required (Ogle 1992).

In an attempt to experimentally determine the salinity requirements for maturation and spawning of *P. setiferus*, the following study was conducted.

### MATERIALS AND METHODS

A small tank maturation system as described by Ogle (1991b) was utilized. Six systems containing six aquaria each with a volume of 120 L were utilized. Three systems contained natural seawater and three systems contained artificial seawater. Salinities of 20, 25 and 30 ppt were tested with both natural and artificial seawater. Bay water

from Davis Bayou in Ocean Springs, Mississippi with a salinity of 25 ppt was heated to 80°C to achieve a 30 ppt salinity through evaporation for use in the three natural seawater systems. This water was then adjusted with well water as required to achieve test salinities. For the artificial seawater systems, Marine Environment (San Francisco, California) artificial sea salt was dissolved in well water and adjusted to the required test salinities.

Female shrimp collected from the wild were held at 30 ppt and 28°C until they had achieved a minimum size of 30 g before being individually placed in an aquarium in one of the six systems. The shrimp placed in the aquaria system had never been matured. Animals were held at 28°C, exposed to a 14L:10D photoperiod and fed a shrimp grower ration (Zeigler, Gardners, Pennsylvania) until they molted.

After molting, the diet was changed to frozen Maine bloodworms, squid and an artificial maturation pellet (Rangen, Buhai, Idaho). Animals were fed three times daily and water temperature and salinity were recorded. Tanks were cleaned daily by siphoning debris from the bottom of the aquaria. Five days after molting, animals were unilaterally ablated by eyestalk enucleation. Egg collectors were placed on tanks containing ablated animals and checked daily. Subsequent molts and time to spawning were recorded. If the animals failed to spawn after four molt cycles, they were discarded. After spawning, animals were replaced with other shrimp from the holding system. As many as 14 shrimp and as few as 7 shrimp were used in the six systems. For each female, the number of days past ablation until the time of spawning was recorded. This data from each system was analyzed using ANOVA. The percent spawning was analyzed using a G-test.

### RESULTS

There were no significant differences in the number of animals that spawned or the time required to spawn between *P. setiferus* at each of the salinities 20, 25 or 30 in

either the natural or artificial seawater. The fewest spawns were recorded for animals held at 25 ppt, while the most spawns recorded occurred at 20 ppt; both were natural seawaters (Table 1). Highest mortality was recorded for animals held in 20 ppt artificial seawater and least mortality for animals held in 30 ppt natural seawater. The earliest spawning occurred seven days past ablation in 20 ppt natural seawater. The latest spawning occurred 58 days past ablation in artificial seawater of 25 ppt. In two of the systems containing natural seawater at 20 ppt, the average

days past ablation was 17, while at 25 ppt the average days past ablation was 28. Even though it appears that best results were obtained for 20 ppt natural and 30 ppt artificial waters, the results were not significantly different. No shrimp in the artificial water with salinities of 20 and 25 ppt spawned during the same molt cycle in which they were ablated. In comparison, 33% and 38% of the shrimp in the natural seawater of 20 and 25 ppt spawned during the same molt cycle in which they were ablated, respectively.

TABLE 1

Effect of Salinity on Maturation and Spawning of *P. setiferus* in Aquaria

| Seawater Type | Salinity ppt | Spawn % | No Spawn % | Dead % | Number | SPAWN        |     |     |                            | SE   |
|---------------|--------------|---------|------------|--------|--------|--------------|-----|-----|----------------------------|------|
|               |              |         |            |        |        | Molt Cycle % |     |     | Average Days Past Ablation |      |
|               |              |         |            |        |        | 1st          | 2nd | 3rd |                            |      |
| Artificial    | 20           | 46      | 28         | 36     | 11     | 0            | 80  | 20  | 27                         | 7.2  |
|               | 25           | 64      | 14         | 22     | 14     | 0            | 56  | 44  | 24                         | 4.26 |
|               | 30           | 50      | 30         | 20     | 10     | 20           | 60  | 20  | 19                         | 3.74 |
| Natural       | 20           | 73      | 9          | 18     | 11     | 38           | 38  | 24  | 17                         | 4.48 |
|               | 25           | 43      | 43         | 14     | 7      | 33           | 33  | 33  | 28                         | 5.70 |
|               | 30           | 54      | 36         | 10     | 11     | 17           | 50  | 33  | 22                         | 4.16 |

Spawns in the same molt cycle as ablation are 1st molt cycle.

### DISCUSSION

*P. setiferus* are thought to spawn in 60 feet of water offshore in Louisiana during May and June when salinities are 34-36 ppt (Lindner and Anderson 1956). Joyce and Eldred (1966) reported the spawning of *P. setiferus* inshore at or near inlets. Bray, *et al.* (1982) caught large numbers of mated *P. setiferus* off Port Aransas, Texas at a salinity of 34 ppt. Marifarms operated with mated females fished from Apalachicola Bay, Florida, but no salinities were reported. Continental Sea Farms, a maturation facility in Florida, utilized water collected at 22-28 ppt and adjusted to 28 ppt salinity. Other reported salinities for maturation of *P. setiferus* are 30.5 to 37.1 ppt, Johnson and Fielding (1956);

44 ppt, Conte, *et al.* (1977); 22 to 30 ppt, Brown, *et al.* (1979); 24 to 29 ppt, Lawrence *et al.* (1980); 30 to 36 ppt, Chamberlain (1988); and 25 to 32 ppt with an average of 26.9 ppt, Browdy and Sandifer (1991).

The results reported here are encouraging and demonstrate that *P. setiferus* can be artificially induced to mature and spawn in lower salinity and artificial seawaters. This may allow production of *P. setiferus* in areas of low salinity and will provide a savings for those facilities utilizing artificial seawater. Further research should be conducted to determine the discrete effects of salinity on mating and egg viability.

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## A NOTE ON THE FINE STRUCTURE OF MYOSKELETAL JUNCTIONS IN *ACARTIA TONSA* DANA (COPEPODA, CALANOIDA)

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### INTRODUCTION

The endoskeleton of the calanoid copepod, *Calanus finmarchicus*, and its muscle attachments were described by Lowe (1935). She reported that the endoskeleton in *C. finmarchicus* consists of two tendinous endosternites and chitinous exoskeletal ingrowths to which muscles are attached. Howse (1960) noted attachments of the main muscles of the thorax to the exoskeleton in *Acartia tonsa*.

Bouligand (1962) described the ultrastructure of muscle attachments to cuticle in three species of freshwater copepods of the genus *Cyclops*. Raymont *et al.* (1974) described the fine structure of muscle attachments to cuticle in *C. finmarchicus*.

Information of the internal anatomy of marine copepods remains sparse. Therefore, we thought it worthwhile to focus our observations on the attachments of muscle to exoskeletal ingrowths in *A. tonsa*.

### MATERIALS AND METHODS

Live specimens of *Acartia tonsa* Dana were fixed overnight in cold phosphate-buffered 3% glutaraldehyde (pH 7.2), washed in cold 0.1 M phosphate buffer (pH 7.2) with 5% sucrose for two hours, and post-fixed in phosphate-buffered 1% osmium tetroxide (pH 7.2) for two hours (Millonig 1961). The specimens were embedded in a Maraglas-Cardolite mixture according to the method of Freeman & Spurlock (1962). Ultrathin sections were cut and doubly stained with uranyl acetate and lead citrate for electron microscopy. These sections were examined and photographed with a Siemens Elmiskop 1A electron microscope.

### RESULTS AND DISCUSSION

Lowe (1935) reported that the muscles in *C. finmarchicus* are attached to the chitinous exoskeletal ingrowths (CEI) by tendinous connections, and that the endosternites are attached to the exoskeleton by "groups of ectodermal tonofibrils." Furthermore, she stated that some of the chitinous ingrowths serve only as attachments

for muscle and "may be regarded as true apodemes comparable with those which Manton (1928) has described in *Hemimysis* as being formed by the gradual sinking in of the attachment of a group of muscle." The muscle attachments to the exoskeleton that we observed in *Acartia* appear to fit this criterion for apodemes. Lowe (1935) stated that the endosternites provide support for the muscles of the antennae and mouth parts. The chitinous ingrowths from the exoskeleton provide attachments for the remaining somatic muscles.

Raymont *et al.* (1974) described muscle attachments in *C. finmarchicus* to a tendon: "Arising from this are fine tubules which become grouped together into electron-dense bundles of fibers with loss of the tubular appearance." They stated that these fibers bridge a narrow space and insert "...into the cuticle as tonofilaments which can be seen with diminishing density for practically the full thickness of the cuticle." Further, they found no specialized tendinous attachments in some areas. However, the sarcolemma of the muscle cell is apposed to the hypodermal membrane. But there are no tubular fibers in the hypodermis or tonofilaments penetrating the cuticle.

Slight variations occur in the diameter of microtubules (MT) among different species. They are over 280 Å in diameter in the brown shrimp, *Penaeus aztecus* (Talbot *et al.* 1972), about 210 Å in diameter in the horseshoe crab, *Limulus polyphemus* (Sherman 1974), 240 Å in the crab, *Carcinus maenas* (Roosner and Sherman 1976) and about 230 Å in the insects, *Calpodes ethlius* and *Rhodnius prolixus* (Lai-Fook 1967).

*Acartia* epidermal cells (tendinal cells, TC) are interposed between the chitinous exoskeletal ingrowth (apodeme) and the muscle cell (Figs. 1,2,3) where they form the tendo-skeletal junction with the former and the myotendinal junction with the latter. The gap of the myotendinal junction is from 160 to 230 Å in width (Fig. 1), narrower than a similar gap in the copepod, *Cletocampus retrogressus*, in which it is 400 Å (Gharagozlou-van Ginneken and Bouligand 1973), and in *P. anemoniae* in which it is 300 to 400 Å wide (Brigg, 1979). A similar gap in the barnacles, *Balanus improvisus* and *B. balanoides*, ranges from 250 to 700 Å depending upon the region (Koulish 1973). The membranes of the cells forming the gap in *Acartia* are electron-dense but no desmosomes or other

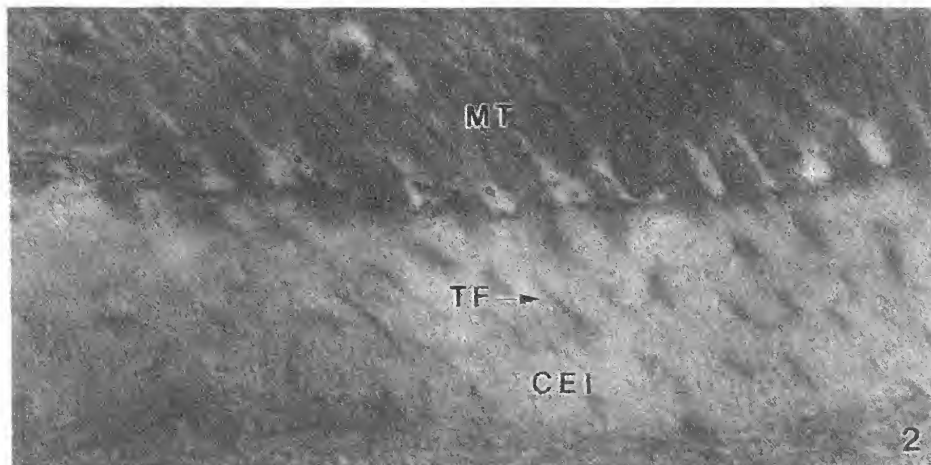
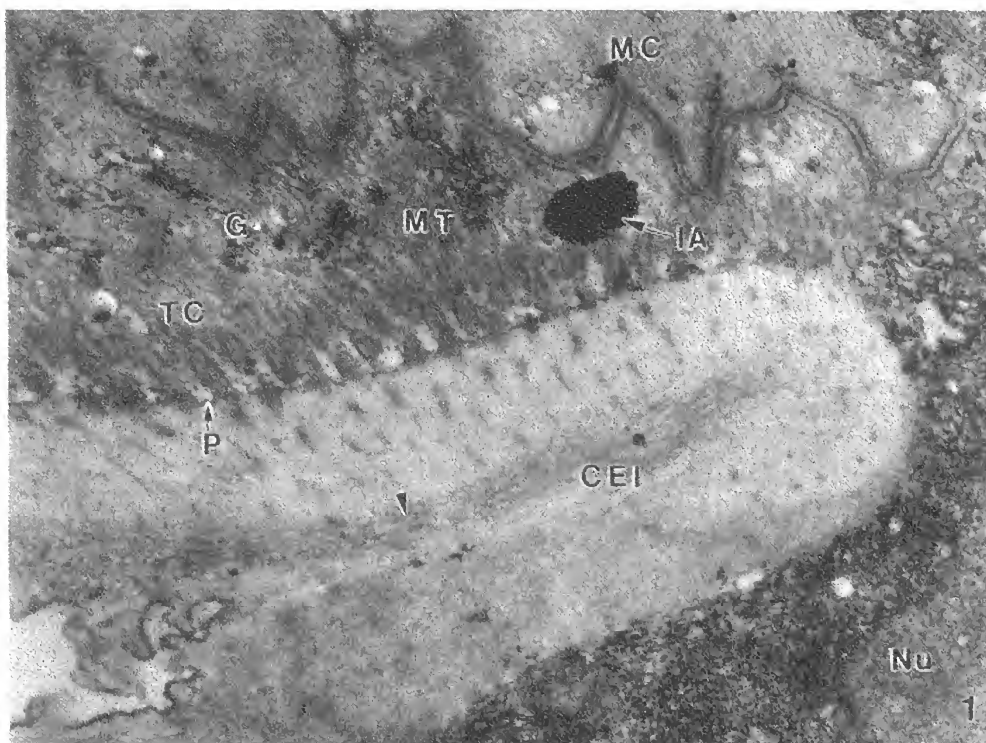


Figure 1. Section through an epidermal tendinal cell (TC) interposed between the distal end of a muscle cell (MC) and a chitinous exoskeletal ingrowth (CEI). The microtubules (MT) are shown in longitudinal view, most of which are bent. Note the several layers of chitin (arrowhead) in the center of the CEI. G-glycogen; IA-irremovable artifact; Nu-nucleus; P-plasmalemma. X 43,500.

Figure 2. Higher power view of the MT as they attach to cuticular projections, and the tonofibrils (TF) penetrate and ramify within the CEI. X 104,400.

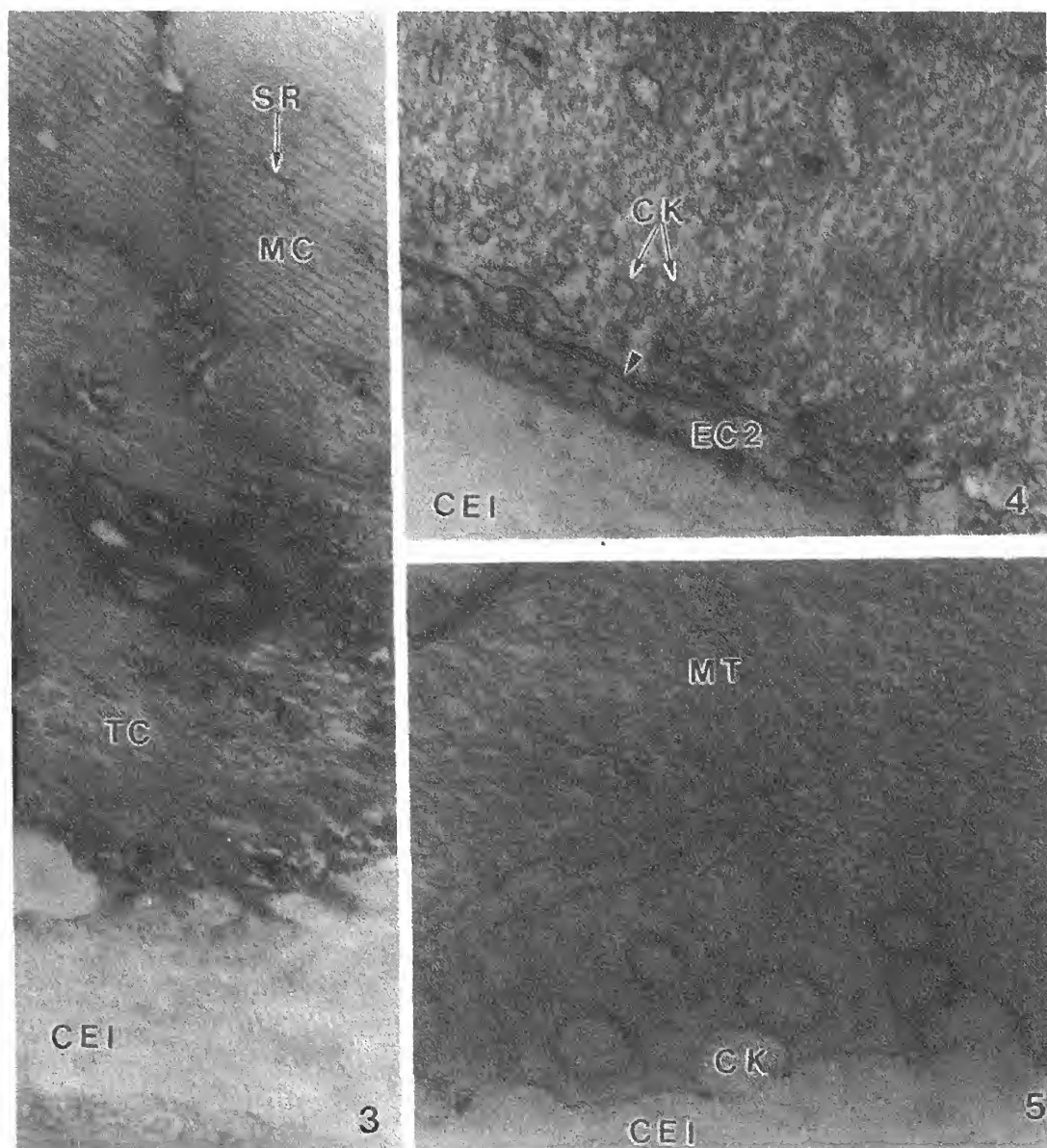


Figure 3. Section of an obliquely attached epidermal tendinal cell (TC) to the exoskeletal chitinous ingrowth (CEI). MC-muscle cell; SR-sarcoplasmic reticulum. X 58,000.

Figure 4. Transverse view of the microtubules (MT). Note desmosomal attachment of MTs to chitinous knobs (CK) and their uniform distribution throughout the cytoplasm. Note the intermediate junction (arrow head) between the tendinal cell and an adjacent epithelial cell (EC2). CEI-chitinous exoskeletal ingrowth. X 58,000.

Figure 5. Transverse view of the MTs and large chitinous knobs (CK) indenting the apical plasma membrane of the epidermal tendinal cell. CEI-chitinous exoskeletal ingrowth. X 108,000.

specialized junctions occur.

The cytoplasm of the TCs in *Acartia* contain numerous MTs that are about 230 Å in diameter and extend from their insertion in the basal end of the TC to their insertion in the apical region (Figs. 4,5). The MTs are larger than those in *Cyclops* in which they are 125 to 150 Å in diameter (Bouligand 1962) and in the cyclopoid copepod, *Paranthesius anemoniae*, in which they are 200 Å in diameter (Briggs 1979). In *Acartia* they are dispersed but closely associated throughout the cytoplasm (Fig. 1). They form groups, each of about 800 Å in diameter, and become electron-dense where they attach by hemidesmosomes to cuticular projections that form invaginations in the apical region of the TC (Fig. 2). In some areas, the attachment of the TC to the cuticle is marked by chitinous knobular projections that arise from the cuticle. They vary in diameter up to 1200 Å (Fig. 5). The microtubules of the TC attach to the chitinous knobs by hemidesmosomes (Figs. 2,5). In other areas, the TC appears to be attached to the cuticle by tonofibrils that pass from the core of the invaginations deeply into the cuticle. This finding differs from that in *C. finmarchicus* which in some areas lack tonofibrils and the muscle cell attaches directly to the innermost layer of the cuticle (supra cit.). In other areas, tonofibrils span a narrow space (Raymont *et al.* 1974), and in *Cyclops* (Bouligand, 1962) there is a space between the epidermal cell and the cuticle through which the tonofibrils cross. In *C. maenus*, cuticular rods arise from the cuticle and insert into conical invaginations of the tendinal cell (Roosner and Sherman 1976). Similar groups in *Cyclops* consist of about 10 tonofibrils (Bouligand 1962), and in *P. anemoniae* they

form electron-dense fibers of about 400 nm in thickness (Briggs 1979). The TFs that attach the TC to the cuticle are 0.08 µm in diameter in *C. ethlius* and 0.05 to 0.22 µm in *R. maenus* (Lai-Fook 1967).

In one of our preparations, the MTs are bent, a configuration that may reflect the relaxation or severance of the proximal end of the muscle (Fig. 1).

Close association between adjacent TCs occur near the CEI (Fig. 4). The TCs are nucleated and contain pockets of glycogen (Figs. 1,3). The plasmalemma of the adjacent cells are electron-dense and are separated by a gap of about 140 Å which is bisected by electron-dense material forming intermediate junctions.

The chitinous projections and knobs provide a firm anchor for the TC, the microtubules of which may contribute powerful tensile strength to enable the cell to withstand the force of muscle contraction (Lai-Fook 1967). The tendinal cell not only provides a strong tendinous attachment for the muscle to the exoskeleton, but may also absorb the shock of contraction in this constantly swimming and highly active organism. Neither the chemistry of the tonofibrils nor their functional mechanisms are known, but Dustin (1978) stated that "... they appear to have a mechanical role (in tension)..."

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